The potential yield of fish stocks

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ABSTRACT

This paper reviews the information relating the average sustainable yield (Y) from a fishery resource to the biomass (B_o) present before exploitation starts. By examining the population parameters of a range of fish stocks, and using simulation modelling it has been shown that the commonly used formula $Y = 0.5\ M\ B_o$ gives too high a value for Y. The degree of over-estimation depends on the nature of the stock-recruitment relation, and on the variability of recruitment. The implications for management and survey design are discussed.

CONTENTS

1. INTRODUCTION

The background of this study is concerned with the problem of estimating the potential sustainable yields of fish stocks that hitherto have been unharvested. The need for guidelines for such estimation of yields is obvious. However, this need has been exacerbated by the extension of exclusive economic zones and the considerable interest that this has engendered in coastal states in calculating the potential of their newly acquired resources.

In responding to these demands FAO has been involved in a series of surveys using the R/V Fridtjof Nansen (FAO 1978; Kesteven, Nakken and Stromme 1981) and other vessels (Troadec and Garcia 1980; FAO/UNDP 1981; Vidal-Jünemann 1981). These surveys use a mixture of acoustic and other techniques to produce estimates of the abundance of a particular fish stock. An approximation to the maximum sustainable yield (MSY) of this biomass is then calculated using some simple formula. The most commonly used form is

$$MSY = 1/2\ MB_o$$

where M is the coefficient of natural mortality and B_o the estimated biomass of the fish stock. A variety of other forms have been proposed to take account of previous levels of exploitation and yield curves which reach their MSY at other than 1/2 B_o (Gulland 1971). This approximation to MSY is then used as an indicator of the potential yield of the resource.

In this study we examine the validity of this approximation both in general, and in particular, where it has been used when coupled with research surveys.

It is a beguiling idea that if one knows sufficient of the life history characteristics of a species, it will be possible to make some estimate of its potential for sustaining catches. It is an even more beguiling idea that there is some simple expression which encapsulates that information and permits sustainable yields to be calculated for all species. This in essence is the idea of the so-called production model which subsumes all the details of life history characteristics and density-dependent responses into the single equation in biomass B.

For the Schaefer model the particular form used is

$$\frac{dB}{dt} = rB(1 - B/B_o) \qquad (1)$$

Here the MSY level occurs at half the virgin biomass, B_o, and this feature, coupled with the claim that maximum sustainable yields appear to occur when fishing mortality F is similar to natural mortality M, leads to the use of the expression

$$MSY = 1/2MB_o \qquad (2)$$

as an approximation to the maximum sustainable yield.

Recently Shepherd (1982) has made some similar calculations for more general production models and concluded that the MSY tended to be somewhat less than the expression 1/2 MB_o, but depending on choice of parameters greater values could be obtained.

This use of the expression presupposed that the production model is a reasonable representation of the dynamics of fish stocks. Some check on this can be made by considering equation systems of a more realistic nature. For example a more detailed model may be constructed using the framework of the Beverton and Holt equations and

estimates of sustainable yield can be made for different parameter combinations. Gulland (1971) adopted this approach and reached the broad conclusion that within a reasonable range of parameter values and fishing strategies the use of equation (2) would produce a satisfactory approximation to the maximum sustainable yield predicted by the "simple" (constant recruitment) Beverton and Holt model. This result has led to the use of expression (2) in calculations of the potential yield of a wide variety of fish stocks (Gulland 1971).

There are three major problems with the use of this approximation. Firstly, the analysis of the Beverton and Holt model, considered above, is misleading in that for most realistic choices of an age or size at recruitment the MSY as a proportion of unexploited biomass is rather less than the 1/2 M level. This problem of choice of age at recruitment had been mentioned by Gulland (1971), but was not fully explored by him.

Secondly, harvesting at the MSY level in some cases involves a reduction of the spawning stock biomass to a level where the chance of recruitment declines are significant, hence the assumption of constant recruitment would be likely to be violated. One possibility, explored below, is to constrain the harvest level to ensure that there is some constant escapement.

Thirdly, as is well known, recruitment is highly variable in some fish stocks even when the parent stock is relatively unchanging. This last problem has several implications. Firstly, even though harvesting at MSY may be in some cases be compatible with a given escapement if recruitment were constant, recruitment variation may mean that there is a high probability that there will be a reduction in spawning stock to below this escapement level. Secondly, a quota management system which seeks to harvest a fixed quantity each year, corresponding to the estimated MSY, may lead to unacceptably high variations in fishing mortality and effort. Thirdly, a target effort level based on MSY may produce unacceptably high variation in catch. Fourthly, survey estimates of initial biomass may be misleading as the biomass fluctuates with recruitment, and the surveys may have been made when abundance was uncharacteristically high or low.

The remaining analysis is organised into four sections. In the first the basic Beverton and Holt model is re-examined, and the actual MSY levels for different parameter combinations are presented.

In the second, the effect that MSY harvesting has on the spawning stock is examined and the problem of an appropriate escapement level is discussed.

In the third section the underlying variability of recruitment is considered and the fate of model populations that undergo the process of survey, assessment and harvesting are explored by Monte Carlo techniques. In this section the potential yield calculations are modified to ensure that the probability that a stock will be reduced below some fixed escapement in a particular time span is less than some specified value.

In the final section the results of the analysis are used to suggest a series of calculations that need to be made to assess the potential of an unexploited fish resource.

2. THE BEVERTON AND HOLT MODEL REVISITED

In this section the analysis is developed in a simple form of the Beverton and Holt model.

X_{it} is defined as the numbers of age class i in year t, w_i as the mean weight of age class i. R is the recruitment, w_∞ and K the parameters of the Von Bertalanffy curve, and F and M the coefficients of fishing and natural mortality.

The dynamics in the unexploited state are then given by the equation system:

$$X_{o,t} = R$$
$$X_{i,t} = X_{i-1,\ t-1}\ \exp(-M) \qquad all\ i > 0 \tag{3}$$

With exploitation we define an age at recruitment T_r and the equations are then

$$X_{i,t} = X_{i-1,t-1}\ \exp(-M) \qquad i < T_r$$
$$X_{i,t} = X_{i-1,t-1}\ \exp(-M-F) \qquad i > T_r \tag{4}$$
$$X_{o,t} = R$$

The equilibrium yield Y under constant fishing mortality may be expressed as a slight variation of the yield per recruit expression.

$$Y = R\ F \int_{T_r}^{\infty} \exp(-tM - (t - T_r)F)\ w_t\ dt$$
$$where \quad w_t = w_\infty\ (1 - \exp(-kt))^3 \tag{5}$$

The Fmax value associated with the MSY yield Ymax may then be found simply. Ymax can be expressed as a proportion of the unexploited recruited biomass B_o:

We define $$B_o = R \int_{T_r}^{\infty} w_t\ \exp(-Mt)\ dt \tag{6}$$

$$y = Y_{max}/B_o$$

and proceed to ilustrate the values of y for different values of M, K and Tr, in Figs. 1-5. Superimposed on these graphs we have drawn the line $y = 1/2\ M$ to illustrate the relationship between the supposed approximation to MSY given by equation (2) and the actual values calculated from the Beverton and Holt model. The details of these calculations are given in Appendix 1.

The essential difference between the results obtained here and those considered by Gulland (1971) lie in the interpretation of what is feasible, or realistic, parameter space. In Figs. (1-5) where the values of y lie above the 1/2M line the age at recruitment is high and therefore the defined exploitable biomass is a small proportion of the total biomass. Put in another way, it is possible to obtain yields which are in excess of $1/2MB_o$, as noted by Gulland, however such yields tend to occur in situations with an unrealistic combination of age at recruitment and natural mortality. A corollary of this is that they tend to occur at extremely high levels of fishing mortality and would in practice be probably unrealisable.

One alternative way of illustrating this point is by presenting the yield as a proportion of the total biomass of the resource Figs. 6 - 9. Here, as the age at recruitment becomes large, the yield as a proportion of the total biomass remains small relative to the 1/2M line.

Given these considerations the results are striking. For most realistic values of the parameters, the MSY yield as a proportion of the recruited biomass is well below the 1/2M level.

The degree of overestimation varies somewhat, being greatest for the lower ages at recruitment and the lower values of M/K (the ratio of mortality to growth rate). For some parameter combinations the yield is overestimated by up to 200%.

There are four caveats about these results. The first is that they assume a knife edge recruitment. Partial recruitments will obviously effect the quantitative detail of the yield levels obtained.

Secondly the equations are scaled so that the weight at the age zero is zero. Some stocks have "zero" weights at negative ages. Again such considerations effect the detail of the calulations, however it is clear that the qualitative features of substantial overestimation will remain unchanged.

Thirdly the yield will be affected slightly if there are marked seasonal fluctuations in growth, recruitment and mortality. Preliminary studies indicate that this can effect the potential yield by a maximum of 20%.

Fourthly it should be mentioned for completeness that the Beverton and Holt model, by assuming constant asymptotic recruitment, can be somewhat pessimistic for stocks which have a recruitment declining from a peak as stock size increases. Thus for stocks with a domed stock and recruitment relationship, if the MSY occurs at a stock level near the peak of the recruitment curve the results may underestimate the potential yield.

Despite these caveats, it seems clear that the use of the 1/2 MB_0 expression will lead, in the vast majority of cases, to an overestimation of potential yield. This is despite the fact that the level of yield depends on the assumption that recruitment does not decline with decreasing stock size. This assumption is examined in the next section.

3. STOCK RECRUITMENT PROBLEMS

It is well recognised that certain types of fish species demonstrate a decline in the average levels of recruitment at low stock sizes. The level of spawning stock size at which such declines occur is both variable, and when recruitment fluctuates, difficult to determine. This problem is addressed in some more detail below. Here the possible constraints that may be chosen on escapement and how they are violated in certain circumstances are considered. Firstly we define the average unexploited spawning stock biomass as S_0 and the age at maturity as T_m then from equation (3)

$$S_0 = R \int_{T_m}^{\infty} \exp(-Mt)\, dt \tag{7}$$

and under exploitation the equilibrium spawning stock biomass S will be given by

$$S = R \int_{T_m}^{\infty} \exp(-Mt - (t - T_r)F) w_t \, dt \tag{8}$$

if $T_m > T_r$ and a slight modification if $T_m < T_r$. The ratio of the exploited to unexploited stock size P is by definition

$$P = S/S_o$$

In Appendix 2 the value of this ratio is tabulated for a variety of different ages at recruitment, mortality and growth. These results indicate that for a combination of high ages at recruitment and high mortality rates, harvesting at MSY will lead to a substantial reduction in spawning stock biomass from its unexploited level.

Logically one should move on now to consider the necessary reduction in yield that would ensure that the SSB was not substantially reduced. However, because the Beverton and Holt model has such a flat yield curve, the level of reduction required is, in many cases, rather slight. By contrast the necessary reduction in fishing mortality is substantial. A typical case is illustrated in Fig. 10.

For the situation illustrated in Fig 10a, the MSY is around 11% of the unexploited recruited biomass, a reduction in the fishing mortality from its Fmax value of around 0.52 to about half that level will approximately double the equilibrium SSB, but will only reduce the catch by about 10%. However it should be emphasised that this is a rather artificial result. In Fig 10b the relation between the equilibrium spawning stock and catch level is illustrated. It indicates that very small fluctuations in catch around the MSY level will have large effects on the spawning stock. Accordingly as will be shown below, where recruitment varies randomly these deterministic results are effectively meaningless.

In Table 1 we present a summary of the results obtained so far, for typical values of mortality, growth rate, and ages at maturity and recruitment. The implications of

Table 1

		Age at recruitment								
		0			1			2		
		Mortality Rate			Mortality Rate			Mortality Rate		
K′		.2	.4	.6	.2	.4	.6	.2	.4	.6
	Y/Brec	.042	.067	.090	.049	.085	.125	.058	.112	.180
0.2	Y/BTot	.042	.067	.090	.049	.085	.124	.057	.107	.162
	S/So	.293	.307	.274	.267	.261	.214	.245	.219	.179
	Y/Brec	.055	.084	.110	.068	.116	.167	.085	.163	.256
0.4	Y/BTot	.055	.084	.110	.067	.115	.163	.082	.148	.213
	S/So	.269	.269	.252	.227	.206	.162	.196	.162	.113

MSY levels expressed as a proportion of unexploited recruited biomass (Y/Brec)and as a proportion of the total biomass. (Y/BTot) The levels of equilibrium spawning biomass under harvesting.(S/So) are also shown. The age at maturity for these results is 2 years.

these results may briefly be summarised. In most of the feasible biological situations the maximum yield that can be taken from a stock is well below the level given by $1/2MB_0$. Furthermore and in particular for the high mortality rates, there is a further need to reduce the estimates of potential yield to ensure that the spawning stock biomass is not reduced to a level where recruitment may be expected to decline.

These results are also subject to a caveat. In the analysis, we have made the optimistic assumption that the life history occurs in a sequence in which recruitment to the adult stock is followed by spawning and then harvesting. This means when the age at recruitment is greater than or equal to the age at maturity, that the spawning stock level is kept at a maximum. If harvesting occurs prior, to or during spawning, the effect it has on SSB will be somewhat greater. This is particularly true for stocks with the higher mortality rates.

So far the results have been obtained on the assumption that recruitment is constant. We now proceed to examine the problems raised by variable recruitment.

4. THE PROBLEM OF RECRUITMENT VARIATION

A number of recent studies have examined the variation in recruitment for a variety of fish stocks. The basic work is that of Hennemuth, Brown and Palmer (1980), and subsequent analysis has little extended their conclusions. These conclusions are, that recruitment is highly variable for some stocks and tends to possess a skewed frequency distribution, the log normal being a reasonable empirical fit.

In Table 2 we present the results of an analysis of a variety of data sets in which the recruitment variation is presented as the variance of the log normal distribution. This statistic has the advantage of being comparable across data sets with different absolute levels of recruitment. In the subsequent analysis we use the square root of this statistic, that is, the standard deviation of the log-recruitment, which we denote by σ.

The data sets used are, in a sense, self selecting. This is because to obtain information on recruitment variation, a knowledge of the catch at age or length and the natural mortality rate is required. Hence the data are from well studied stocks, for which cohort or virtual population analyses have been performed. To this extent they cannot be considered typical. Furthermore the values of the standard deviation given are only a very approximate guide to the level of variability: recruitment estimates for at least 20 successive years would be necessary to estimate the S.D. to within a factor of two, even if the annual recruitments were mutually independent. In practice years of good or poor recruitment tend to occur together, and so the margin of error in estimating the standard deviation is even greater than this. In all that follows we shall assume that successive annual recruitments are mutually independent provided that the spawning stock biomass is not reduced below some specified minimum level. This assumption will tend to result in an underestimation of the effects of variability.

5. THE IMPLICATIONS OF RECRUITMENT VARIATION FOR ESTIMATES OF POTENTIAL YIELD

There are two basic problems posed by recruitment variation, in estimating the potential yield of fish stocks. The first involves the problem of declining recruitment with stock size. In this situation it is possible that stochastic variation in recruitment will, with high probability, ensure that the SSB will be reduced below some fixed value. This can occur even though in the deterministic case, the equilibrium SSB is above that value.

The second problem is that in the process of survey and assessment of potential yield, the survey is effectively sampling from an underlying probability distribution of the biomass of the fish stock. Hence if the biomass is at an uncharacteristically high level, potential yield could be overestimated, or conversely, underestimated, if the biomass is uncharacteriscally low.

Table 2: Summary of data on recruitment and life history parameters for named fish stocks

CLUPEIFORMES	FAO AREA	AREA	AV. LOG. REC	VARIANCE	L	K	M	T_M	REF. NO.
Clupea harengus	27	(ICES 6A)	20.7	0.51	29.5	0.39	0.1	3	34, 30
Clupea harengus	27	('Isle of Man')	18.3	0.27	29.5	0.39	0.1	3	8, 30
Clupea harengus	27	(Iceland (Spring))	19.8	0.40	36	0.21	0.1	3	23, 30
Clupea harengus	27	(Iceland (Summer))	19.2	0.85	36	0.21	0.1	3	23, 30
Clupea harengus	27	(North Sea)	22.6	0.23	30	0.38	0.1	3	18, 30
Clupea harengus	21	(Georges Bank)	21.3	0.23	34.5	0.34	0.2	3	4, 38
Clupea harengus	21	(North West Atlantic)	22.1	0.41	35	0.33	0.2	3	37, 31
Sardinops caerulea	77	(California)	20.5	0.59	29.3	0.45	0.4	2	28, 27, 31
Sardinops ocellata	47	(ICSEAF 1.6)	22.9	0.50	30.6	0.22	0.5	2	14
Engraulis ringens	87	(Peru, 5-16 S)	19.4	0.37	15.6	1.38	1.5	1	13, 31
Engraulis capensis	47	(ICSEAF 1.6)	24.8	0.10	14.7	0.45	0.8	1	14
Engraulis capensis	47	(ICSEAF 1.3 1.4, 1.5)	24.3	0.13	14.7	0.45	0.8	1	12, 14
Etrumeus teres	47	(ICSEAF 1.6)	21.6	0.38	26.1	0.33	0.5		14
Brevoortia tyrannus	21	(NW Atlantic)	21.5	0.48	37.7	0.24	0.5	3	25, 31, 35
PLEURONECTIFORMES									
Limanda ferruginea	21	(NAFO 3LNO)	11.2	0.07	50	0.33	0.3	2-3	9, 30
Hippoglossoides platessoides	21	(NAFO 3NLO)	12.1	0.07	72	0.1	0.2		32, 31
Pleuronectes platessa	27	(ICES 7DE)	15.1	0.20	70	0.08	0.1	4	19, 29
Pleuronectes platessa	27	(ICES 7DC)	15.0	0.20	45	0.15	0.15	4	19, 30
Pleuronectes platessa	27	(North Sea)	19.0	0.09	70	0.08	0.1	4	19, 30
Pleuronectes platessa	27	(North Sea)	19.0	0.14	45	0.11	0.1	4	19, 30
Solea vulgaris	27	(ICES 7E)	14.2	0.15	37.7	0.42	0.1	3	19, 30
Solea vulgaris	27	(ICES 7E)	14.1	0.19	37.7	0.42	0.1	3	19, 30
Solea vulgaris	27	(ICES 7D)	14.9	0.29	37.7	0.42	0.1	3	19, 30
Solea vulgaris	27	(North Sea)	17.6	0.55	37.7	0.42	0.1	3	19, 30
Solea vulgaris	27	(North Sea)	17.8	0.63	" "	" "	0.1	3	19, 30
Reinhardtius hippoglossoides	21	(NAFO 23 KL)	11.7	0.10	-	-	0.2	11	5, 7
GADIFORMES									
Gadus morhua	21	(NAFO 3NO)	11.1	0.43	130	0.12	0.2	3	6, 31
Gadus morhua	21	(NAFO 3M)	9.9	0.97	98	0.15	0.2	3	15, 31
Gadus morhua	21	(NAFO 2JKL)	8.3	0.36	67	0.28	0.2	3	40, 31
Gadus morhua	21	(NAFO 1)	10.9	1.10	90	0.23	0.2	3	16, 31

Table 2 - cont.

GADIFORMES	FAO AREA	AREA	AV. LOG. REC.	VARIANCE	L	K	M	T_M	REF. NO.
Gadus morhua	21	(Georges bank & Gulf of Maine)	17.1	0.07	146.5	0.11	0.2	3	36, 38
Gadus morhua	27	(NE Arctic)	13.5	0.71	156	0.07	0.2	8	17, 31
Gadus morhua	27	(ICES 6A)	8.8	0.20	126	0.21	0.2	3	20, 31
Gadus morhua	27	(North Sea)	12.2	0.42	132	0.2	0.2	3	20, 31
Melanogrammus aeglefinus	27	(ICES 6A)	10.5	1.83	43	0.26	0.2	3	20, 31
Melanogrammus aeglefinus	27	(North Sea)	14.4	1.14	53	0.2	0.2	3	20, 31
Melanogrammus aeglefinus	27	(NE Arctic)	12.0	1.22	115	0.0084	0.2	8	17, 31
Melanogrammus aeglefinus	21	(Georges bank)	17.3	2.84	72.9	0.35	0.2	3	11, 38
Pollachius virens	21	(Scotian shelf to Southern NE)	17.5	0.10	97.7	0.21	0.2	5	10, 38
Pollachius virens	27	(NE Arctic)	13.2	0.15	107	0.19	0.2	6	21, 31
Pollachius virens	27	(Iceland)	12.6	0.27	120	0.15	0.2	5	21, 31
Pollachius virens	27	(Faroes)	10.4	0.15	120	0.15	0.2	5	21, 31
Pollachius virens	27	(North Sea)	12.4	0.30	107	0.19	0.2	5	21, 31
Pollachius virens	27	(W Scotland)	10.8	0.07	107	0.19	0.2	5	21, 31
Urophycis chuss	21	(Scotian Shelf)	19.1	0.11	42.6	0.37	0.4	2	2, 38
Urophycis chuss	21	(Georges bank)	19.4	0.37	42.6	0.37	0.4	2	2, 38
Micromesistius poutassou	27	(ICES 6A)	11.4	0.62	39.9	0.15	0.2	3	20, 31
Micromesistius poutassou	27	(North Sea)	14.8	0.18	33.4	0.23	0.2	3	20, 31
Merluccius bilinearis	21	(Georges bank)	20.6	0.44	50.7	0.24	0.4	2	1, 38
Merluccius bilinearis	21	(Gulf of Maine)	19.3	0.75	65.4	0.18	0.4	2	1, 38
Merluccius bilinearis	21	(Mid Atlantic)	20.2	0.41	46.0	0.41	0.4	2	1, 38
Merluccius bilinearis	21	(NAFO 3NLO)	14.0	0.47	94		0.4	2	39
Merluccius capensis & paradoxus	47	(ICSEAF 1.3, 1.4)	20.4	0.42	110.7	0.14	0.3	2	33, 24
Merluccius capensis	47	(ICSEAF 1.3, 1.4)	21.2	0.11	111.1	0.12	0.3	2	22, 24
Merluccius capensis	47	(ICSEAF 1.5)	20.5	0.14	125.2	0.10	0.3	2	22, 24
Merluccius capensis	47	(ICSEAF 1.6)	20.2	0.16	118.8	0.11	0.3	2	22, 24
PERCIFORMES									
Scombridae									
Scomber scombrus	21	(NAFO 2-6)	21.1	0.74	41.4	0.25	0.3	2	3, 38
Scomber japonicus	77	(Pacific)	12.6	1.21	40.4	0.22	0.5	2	29
Scomber japonicus	47	(ICSEAF 1.6)	18.1	1.34	66.0	0.20	0.25	3	14
Carangidae									
Trachurus trachurus	47	(ICSEAF 1.3/4)	24.6	0.19	54.2	0.12	0.4	3	26, 14
Trachurus trachurus	47	(ICSEAF 1.6)	19.4	1.5	54.2	0.12	0.25	3	14

In analysing these two problems we have related them, by investigating, using Monte Carlo techniques, the whole process of survey, assessment and harvesting. In this way we can assess the probability that the stock will be reduced to some constraint level under different levels of harvest.

The basic question that can be answered from the Monte Carlo investigations is 'What is the probability that the spawning stock biomass will drop below some specified escapement level in a fixed period of time?' However to pose the question in the context of assessing potential yields we have asked the question. 'What modification of the basic catch level will ensure that this probability is less than some specified amount?'

In order to gain some insight into the process, prior to considering the stochastic system, it is useful to consider the dynamics of the deterministic case. Once harvesting begins, the stock biomass will follow a pattern of the type illustrated in Figure 11. Harvesting at a constant fishing mortality will give catches which are initially large, but which decline rapidly as the population moves towards the new equilibrium. By contrast, the operation of a constant catch quota will require initially a small fishing mortality, which will necessarily be increased towards a maximum as the equilibrium biomass is approached. The approach to equilibrium in this case will be slow relative to the constant fishing mortality strategy.

The biological characteristics of the resource also have an effect on the speed of approach to the equilibrium. The mortality rate, and to a lesser extent the von Bertalanffy growth coefficient, determine the time scale of the response to exploitation. When both are high the approach to equilibrium is rapid, when both are low, it may take two or more decades.

Superimposed on this deterministic process are the two stochastic factors caused by recruitment variation. One affects the initial biomass and hence, in absolute terms, the level of harvest attempted; the other directly affects the population dynamics as exploitation progresses. We now explore the consequences of this variation.

In a system where recruitment is stochastic, instead of an unexploited equilibrium stock size, there is a probability distribution of recruited population biomass. The expected value of that distribution is

$$E\,(B_o) = R \int_{T_r}^{\infty} \exp(-Mt)\; w_t \; dt \qquad (9)$$

where R is the mean recruitment rate, and its variance is:

$$\mathrm{var}\,(B_o) = v \int_{T_r}^{\infty} \exp(-2Mt)\; w_t^2 \; dt \qquad (10)$$

where v is the variance of the recruitment rate. We ignore here possible year-to-year variations in the growth and mortality rates, in practice these variations exist, but have much less effect these recruitment variations.

In a similar way the expected values of the spawning stock biomass can be written down once the age at sexual maturity is specified. It is then possible to specify some escapement constraint. In all the results that follow, an escapement level of 20% of the expected unexploited spawning stock biomass is used. This is not a conservative figure, but it represents a lower limit where recruitment declines might be expected to be observable. The time scale that has been used is similarly arbitrary, although its choice has been guided by common sense. We have chosen a twenty year period in which to investigate the probability that the escapement will fall below the 20% level.

In presenting the results of this analysis, we have calculated the appropriate level of catch, that will ensure that the probability that the SSB falls below 20% of its unexploited level is less than 0.1.

As we have already indicated. The different strategies of a constant catch and a constant fishing effort have rather different dynamic consequences and hence it is necessary to present the results in two different ways.

5.1 Constant Catch

The calculations here are presented as modifications of the basic deterministic results presented earlier. In Figs (12 -15) the results of the Monte Carlo investigations have been analysed so that the catch level that can be taken as a proportion of the initial surveyed biomass is presented as a function of mortality, growth and the age at recruitment. This catch level is the maximum one that ensures that the probability that the SSB will be reduced to less than 20% of its expected level* in 20 years is less than 0.1.

In all the calculations we have used an age at sexual maturity of two. This will be either accurate, or optimistic, for most fish stocks. However for fish stocks with mortality rates in excess of 0.5, the results will be pessimistic as such stocks typically mature at an age less than two.

The results indicate that for higher levels of recruitment variation it may be necessary to further adjust the catch level downwards to ensure that SSB remains above its constraint level. Table 3 summarises these results.

5.2 Constant Fishing Mortality

The results obtained for a strategy involving constant fishing mortality are not directly comparable to those that can be presented for constant catch. Instead the process needs to be considered in two stages. Figs. 16 - 19 illustrates the reductions in fishing mortality from Fmax that are required to satisfy the constraint that the probability that the SSB will fall below this level within 20 years should be less than 0.1.

The results are illustrated for different values of recruitment variability, mortality, growth and age at recruitment. Associated with each set of these parameters and constraints is a fishing mortality rate. If applied to the stock this fishing mortality rate produces a catch level that reduces as the equilibrium is approached.

Figs. 20 - 23 illustrate these changing expected catch levels. The results show that the constraints on the SSB involve substantial sacrifices in the initial catch compared with those obtainable from fishing at Fmax, but no or only modest sacrifices in the longer term catch.

In Figs. 24 - 25 the approximate confidence regions around some of these expectations are presented. They indicate that where the recruitment variation is large, variation in catch is so great that the practicality of operating a constant fishing mortality is questionable.

In Table 4 the results of the calculations on the strategy of constant fishing mortality are summarised.

* This expected level is defined in equation (9) and may best be considered as the long term average abundance of the fish stock in its unexploited state.

Table 3

Constant catch strategy

Age at recruitment / sexual maturity

		1			2		
		Mortality Rate			Mortality Rate		
K′		.2	.4	.6	.2	.4	.6
	unconstrained	.049	.085	.125	.058	.112	.180
0.2	σ = 0.4	.049	.082	.104	.058	.104	.149
	σ = 1.0	.049	.077	.084	.058	.092	.104
	unconstrained	.068	.116	.167	.085	.163	.256
0.4	σ = 0.4	.068	.101	.129	.085	.139	.200
	σ = 1.0	.068	.086	.092	.085	.106	.110

MSY levels expressed as a proportion of the mean unexploited recruited biomass subject to the constraint that the probability spawning stock biomass falling below 20% of its initial level within 20 years after the start of fishing at a constant catch level is less than 0.1, with two levels of recruitment variability, σ (see text). The unconstrained MSY is shown for comparison.

Table 4

Constant fishing mortality

Age at Recruitment

		0			2		
		Mortality Rate			Mortality Rate		
		.2	.4	.6	.2	.4	.6
K′							
	unconstrained	.042	.067	.090	.058	.112	.180
0.2	σ = 0.4	.042	.067	.090	.058	.108	.173
	σ = 1.0	.041	.061	.072	.055	.092	.121
	unconstrained	.055	.084	.110	.085	.163	.256
0.4	σ = 0.4	.055	.084	.109	.084	.163	.236
	σ = 1.0	.052	.069	.075	.073	.112	.131

MSY under a constant F strategy: the figures represent the maximum long-term yields (as a proportion of average unexploited biomass) subject to the constraint that the probability of the spawning stock biomass being reduced to below 20% of its average unexploited level within 20 years is less than 0.1. Two values of recruitment variability, σ , are used and the unconstrained MSYs shown for comparison. Age at sexual maturity 2 years.

6. THE IMPLICATIONS FOR-SURVEY DESIGN

It is immediately obvious that there is one major implication of the analysis. Clearly future surveys should, in addition to estimating biomass, attempt at least to obtain sufficient samples to estimate the parameters of growth and mortality. Information on recruitment variability is also important, and where a species is relatively long lived, some idea of this can be obtained from the same age/length samples required to estimate the other parameters.

7. THE CALCULATION OF POTENTIAL YIELD FROM A SURVEY

The whole of the foregoing analysis can now be encapsulated in a series of calculations and checks that are needed to estimate a reasonable range for the potential yield of a fish resource.

(1) Given information on the biomass, mortality and growth, a range of estimates of the MSY can be obtained for a chosen age of recruitment. This can be done using Figs. 1 - 5 or Appendix 2 Table 1.

(2) A check should then be made to see if such a level of catch would be likely to reduce the SSB below some target level. This can be done using Appendix 2 Table 3.

(3) The level of recruitment variation to be expected from such a species should then be considered. Often this will need to be done by analogy with similar species in other, hopefully, similar areas.

(4) Given a level or range of recruitment variation the modification in catch level for a constant catch strategy can be calculated. This can be done using Figs. 12 - 15*

A parallel calculation can be made for a constant fishing mortality strategy. The short term and long term catch levels to be expected can then be obtained by inspecting Figs. 20 - 23.

(5) The potential yield of the stock can then be presented as a range calculated for the different strategies of constant catch and constant fishing mortality. Where considerations of a decline in spawning stock size are irrelevant these two strategies will lead to similar results.

It should be emphasised that the estimates obtained in this way are approximate. Indeed even where parameters can be estimated directly, if the full range of uncertainty is considered the yield will usually estimated only to within a factor of two or more.

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* These figures have been constructed, as already discussed, on the basis that the probability of a SSB decline to below the constraint level, is less than 0.1, in a 20 year period.

Fig. 1

MSY as a percentage of initial recruited biomass (deterministic calculation)
Age at recruitment zero

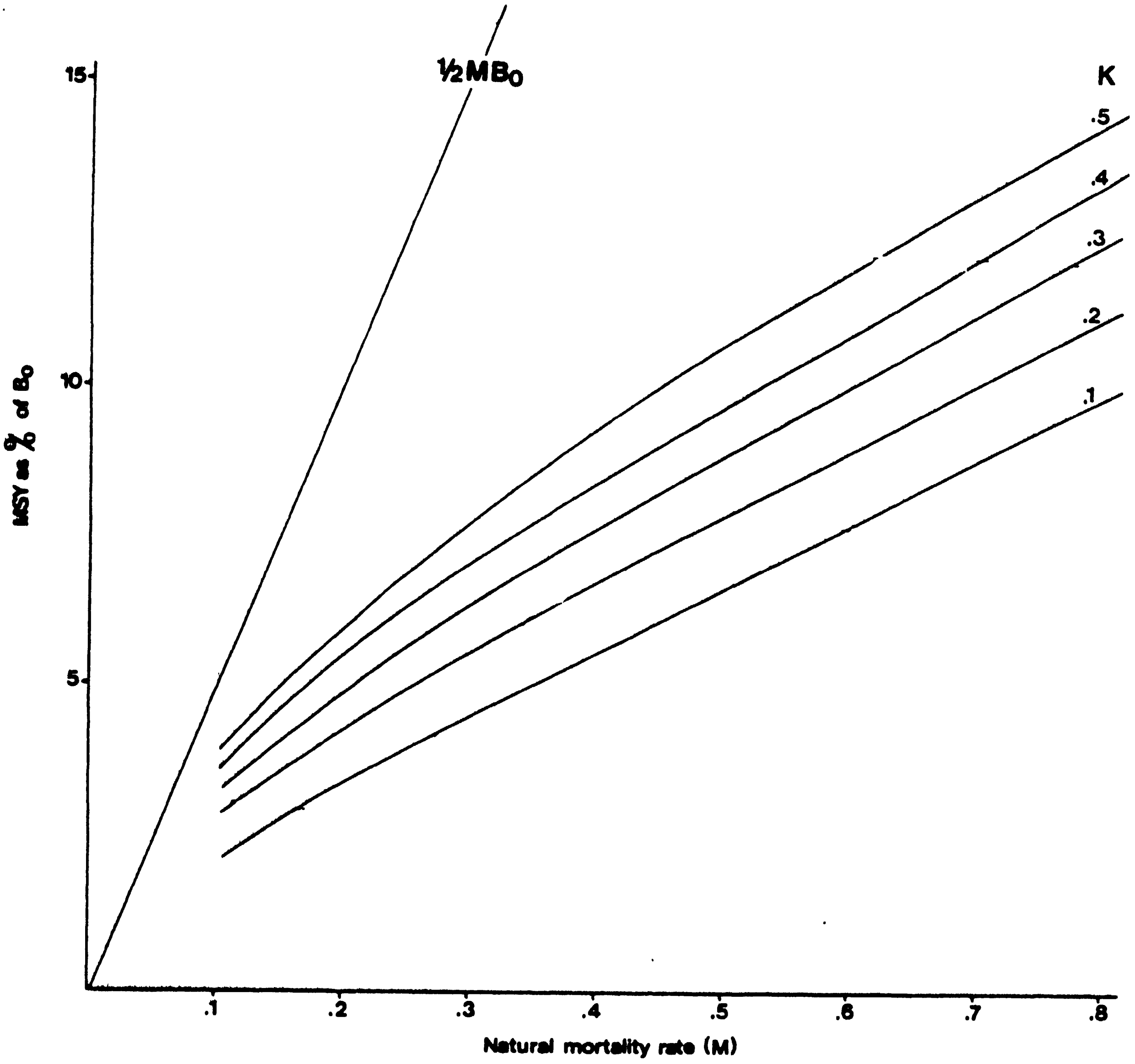


Fig. 2

MSY as a percentage of initial recruited biomass (deterministic calculation)
Age at recruitment 1 year

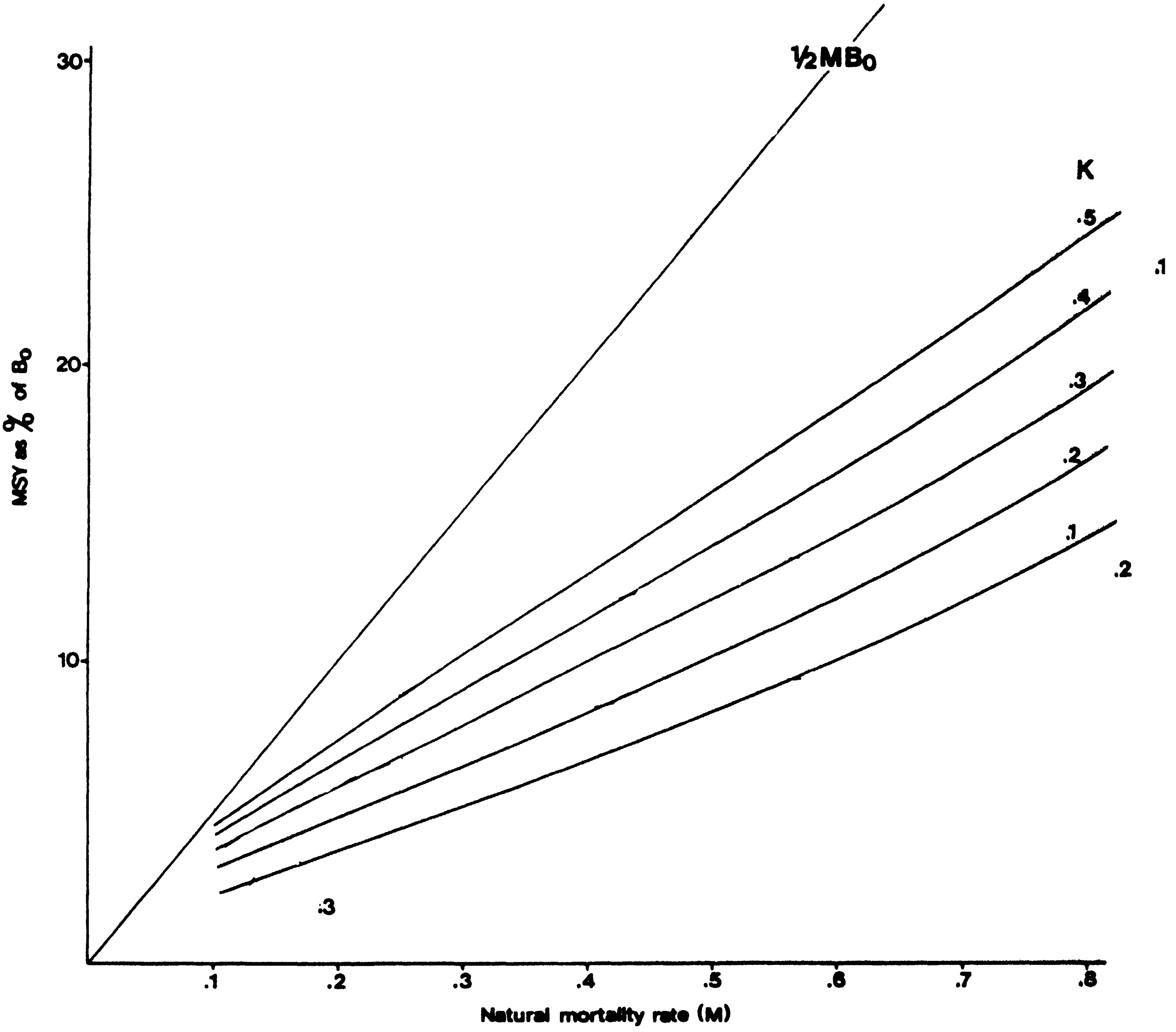


Fig. 3

**MSY as a percentage of initial recruited biomass (deterministic calculation)
Age at recruitment 2 years**

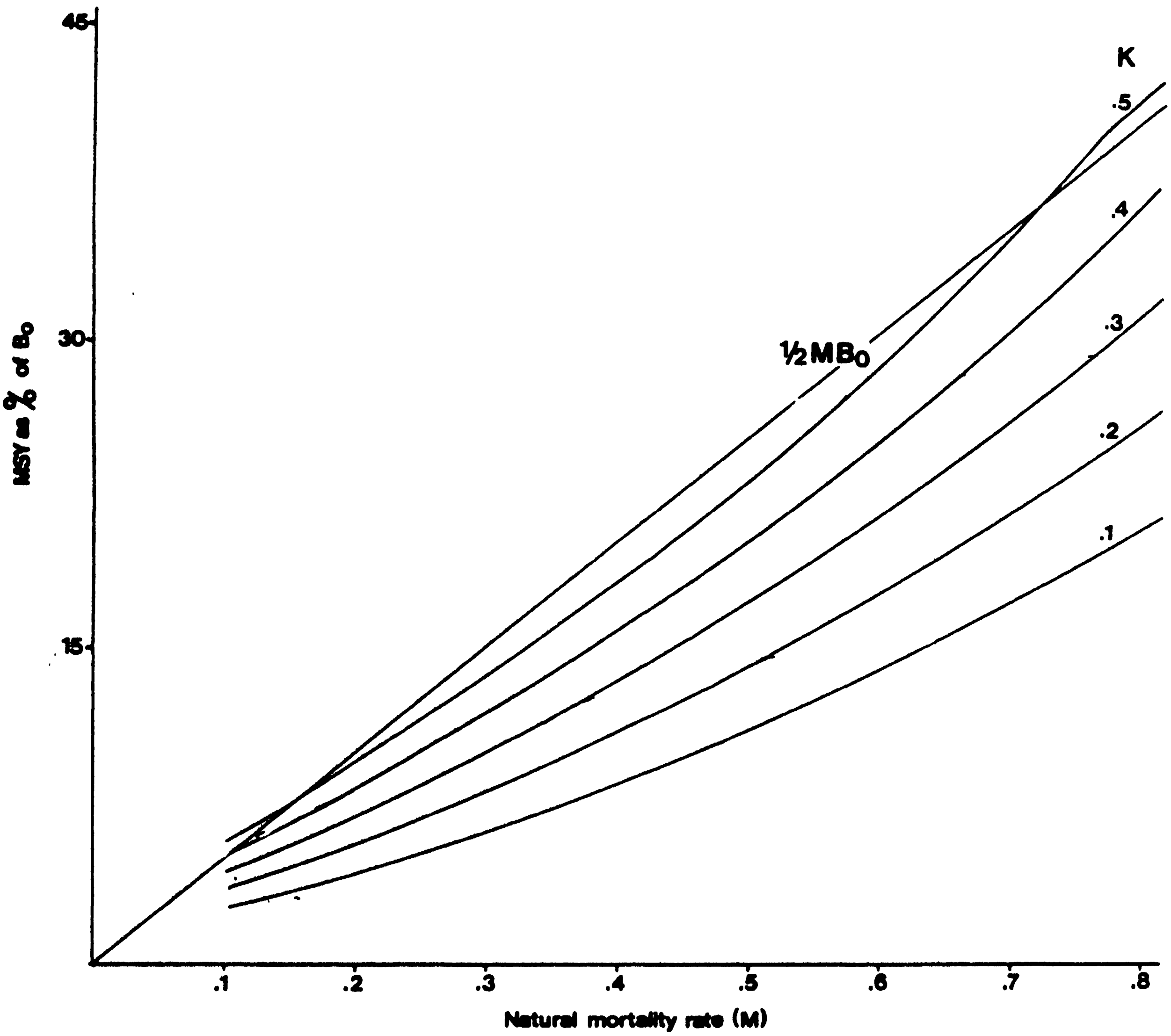


Fig. 4

MSY as a percentage of initial recruited biomass (deterministic calculation)
Age at recruitment 3 years

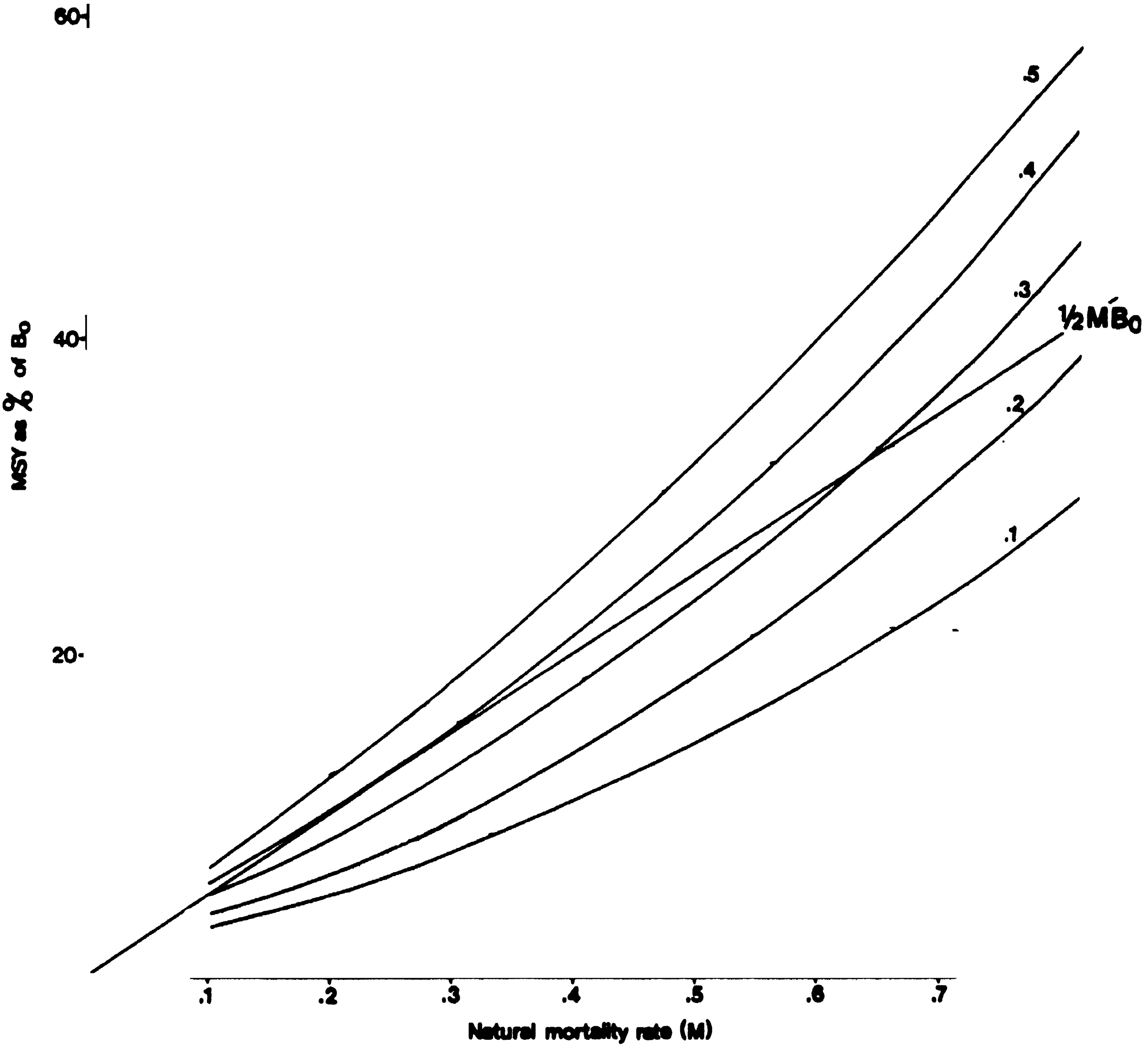


Fig. 5

MSY as a percentage of initial recruited biomass (deterministic calculation)
Age at recruitment 4 years

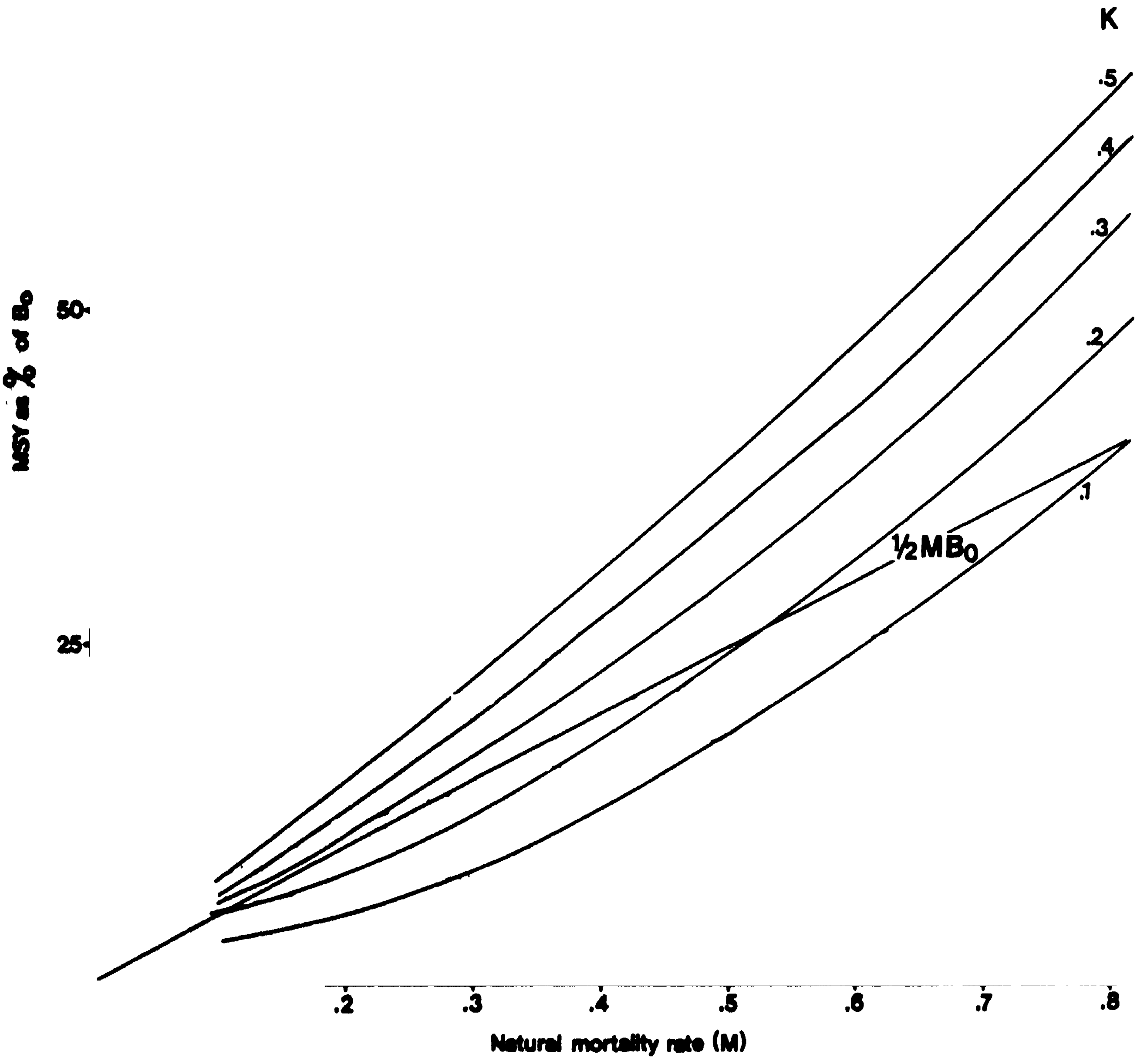


Fig. 6

MSY as a percentage of initial total biomass (deterministic calculation)
Age at recruitment 1 year

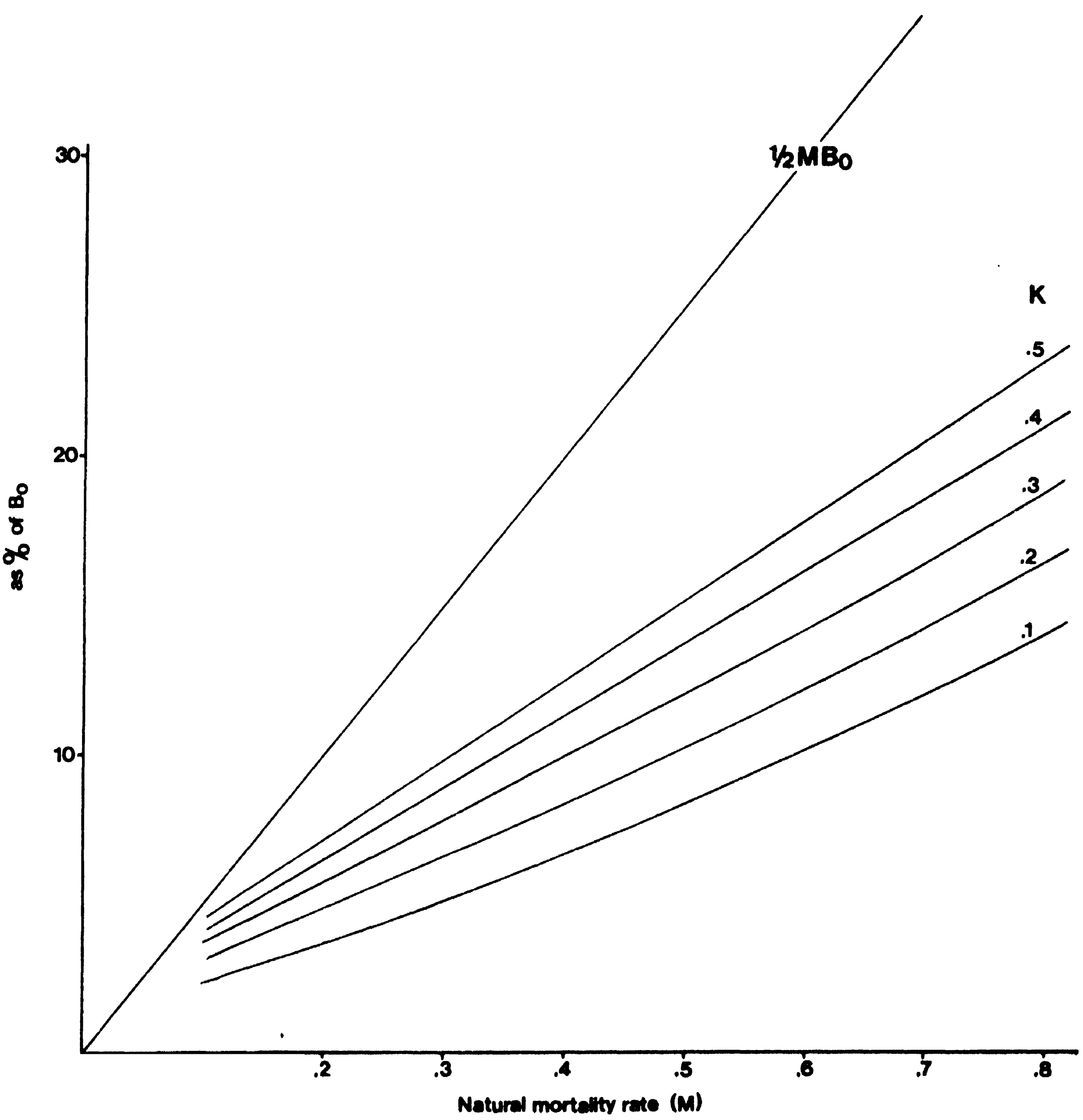


Fig. 7

MSY as a percentage of initial total biomass (deterministic calculation)
Age at recruitment 2 years

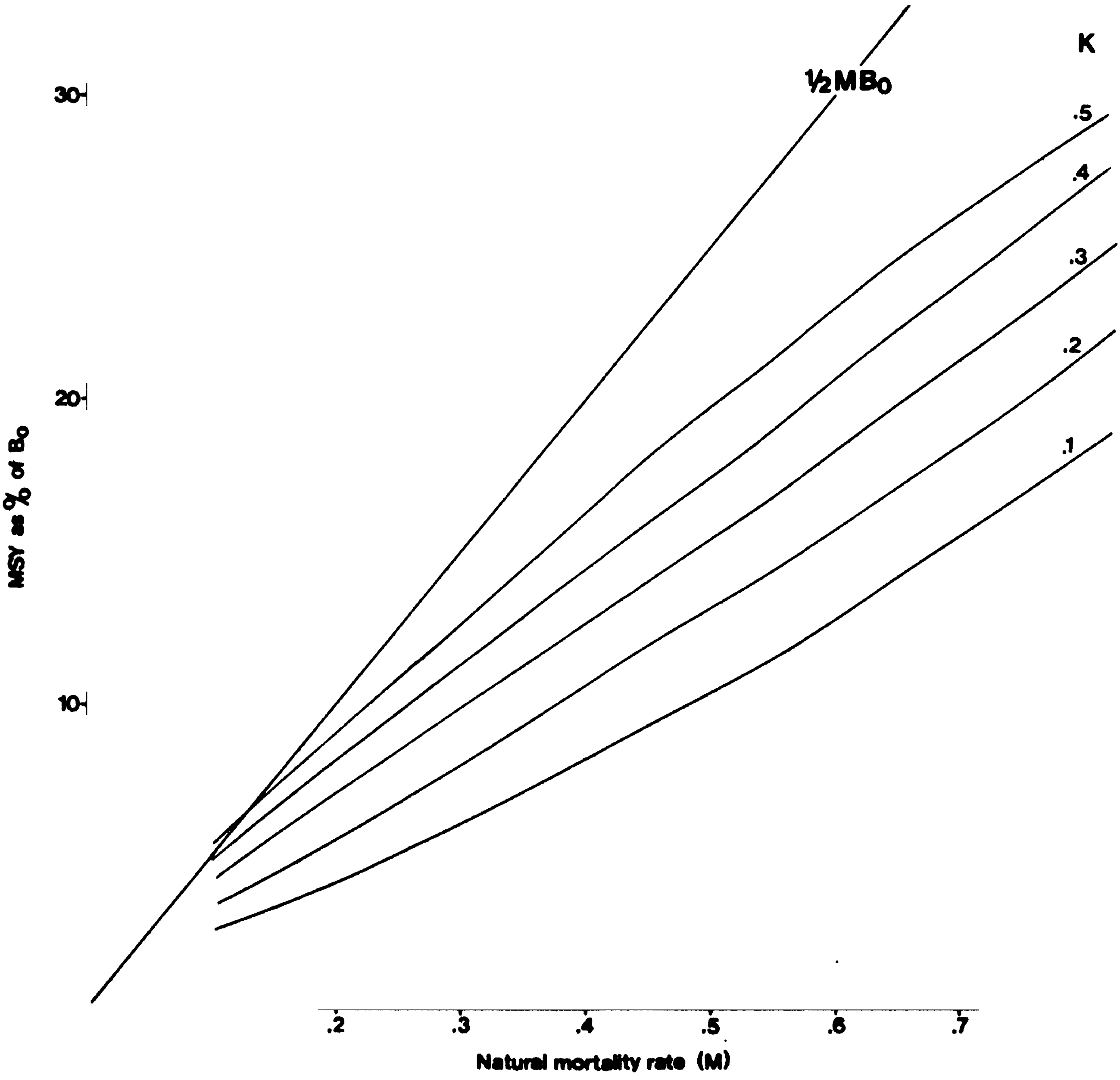


Fig. 8

MSY as a percentage of initial total biomass (deterministic calculation)
Age at recruitment 3 years

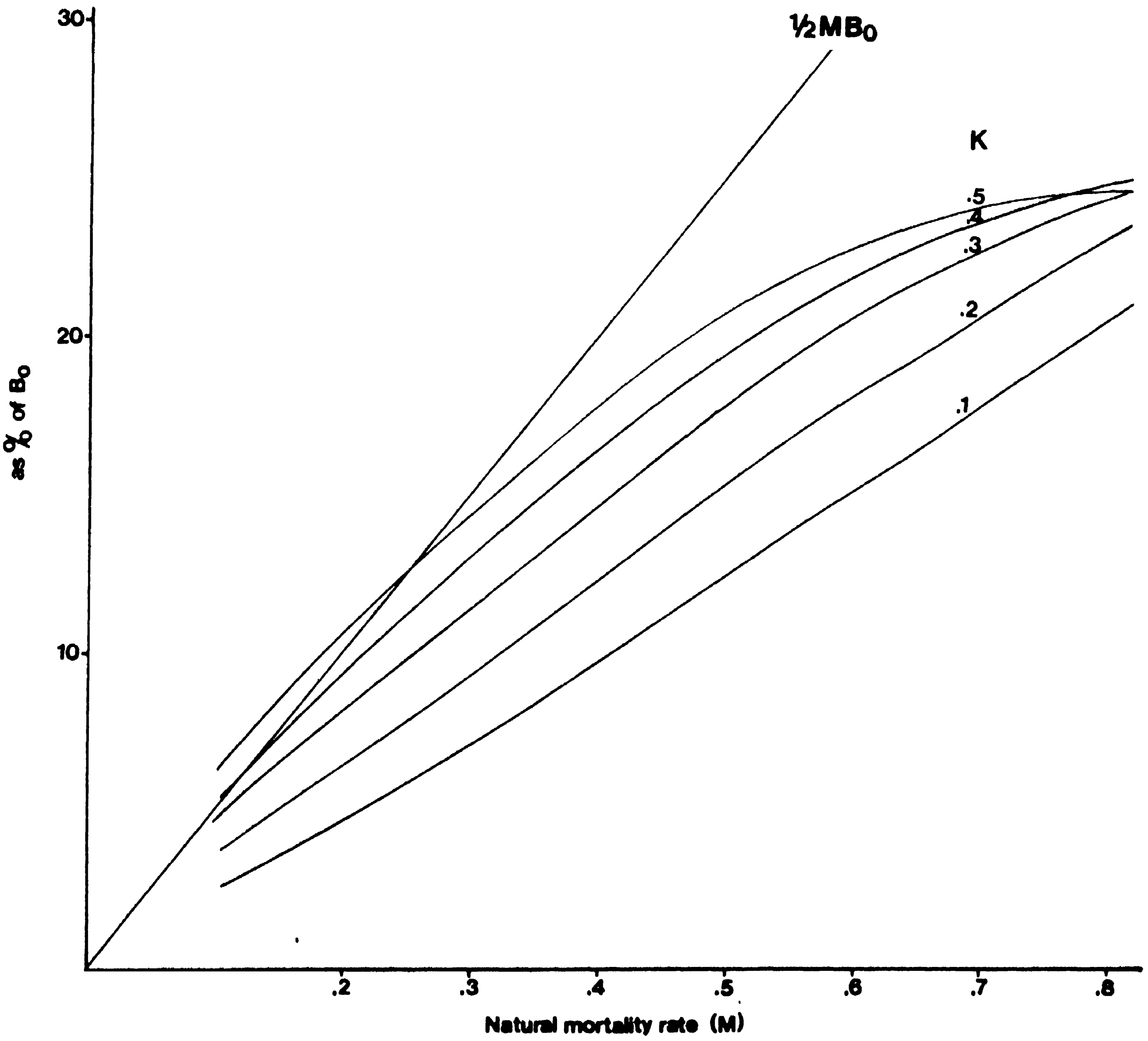
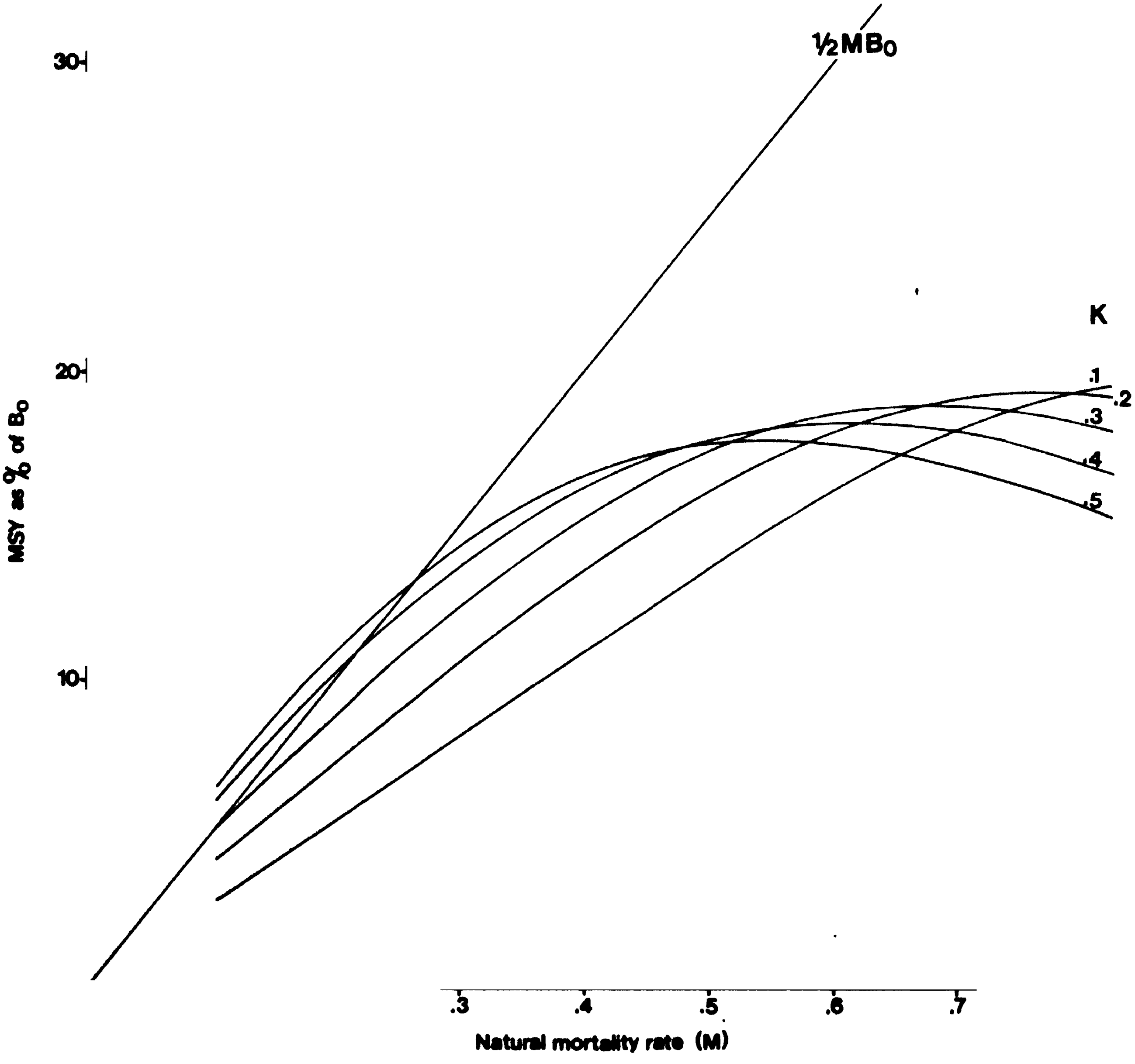


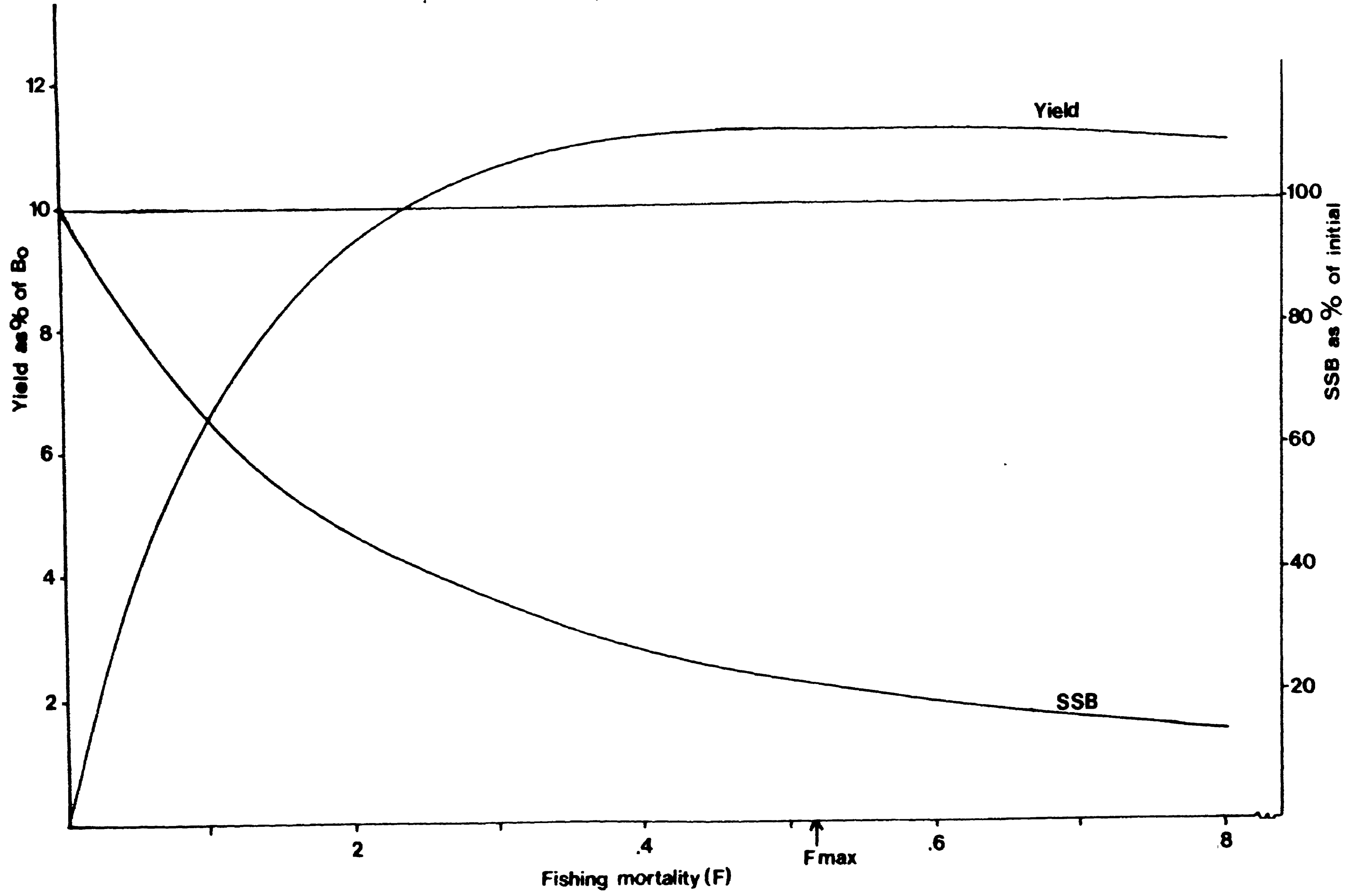
Fig. 9

MSY as a percentage of initial total biomass (deterministic calculation)
Age at recruitment 4 years



g 0a

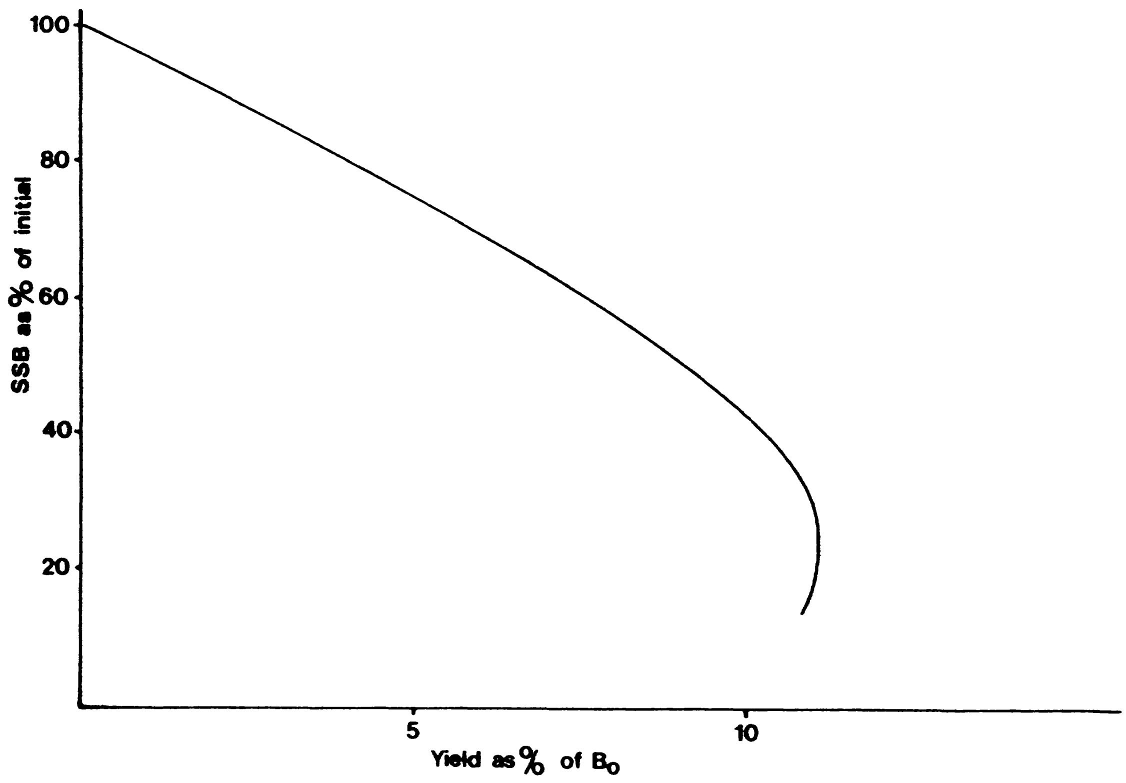
Relationship between Yield, Fishing Mortality
and equilibrium spawning stock biomass.



M= K=.2 Tr=2 Tm=2

Fig. 10b

Relationship between Yield and equilibrium spawning stock biomass.



(M=.4 K=.2 Tr=2 Tm=2)

Fig. 11

Schematic relationship showing decline in Biomass under constant catch and constant Fishing Mortality.

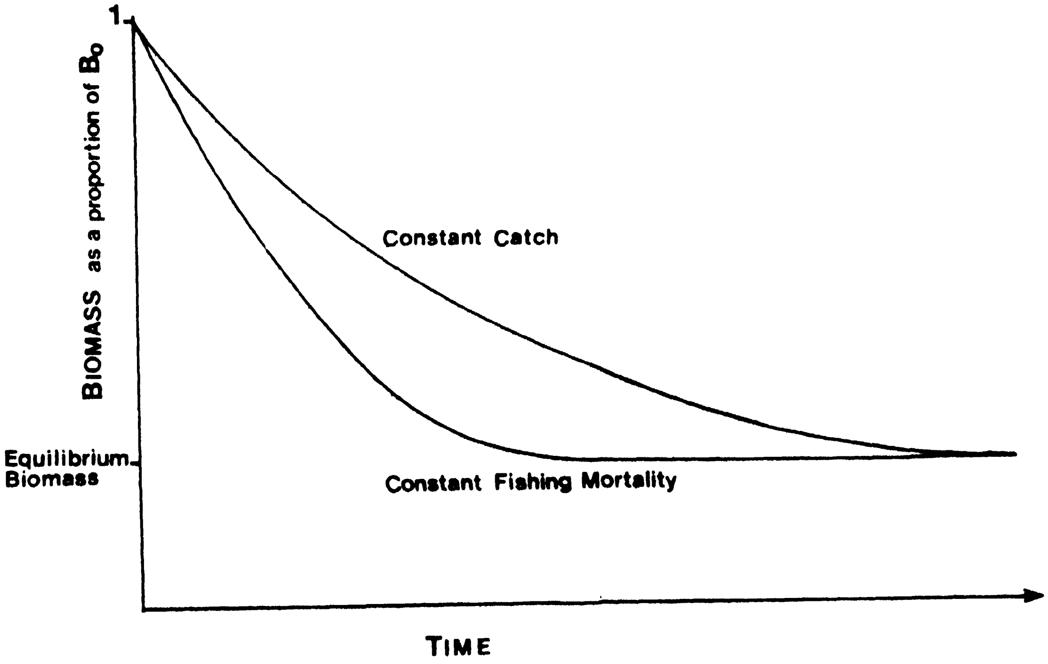
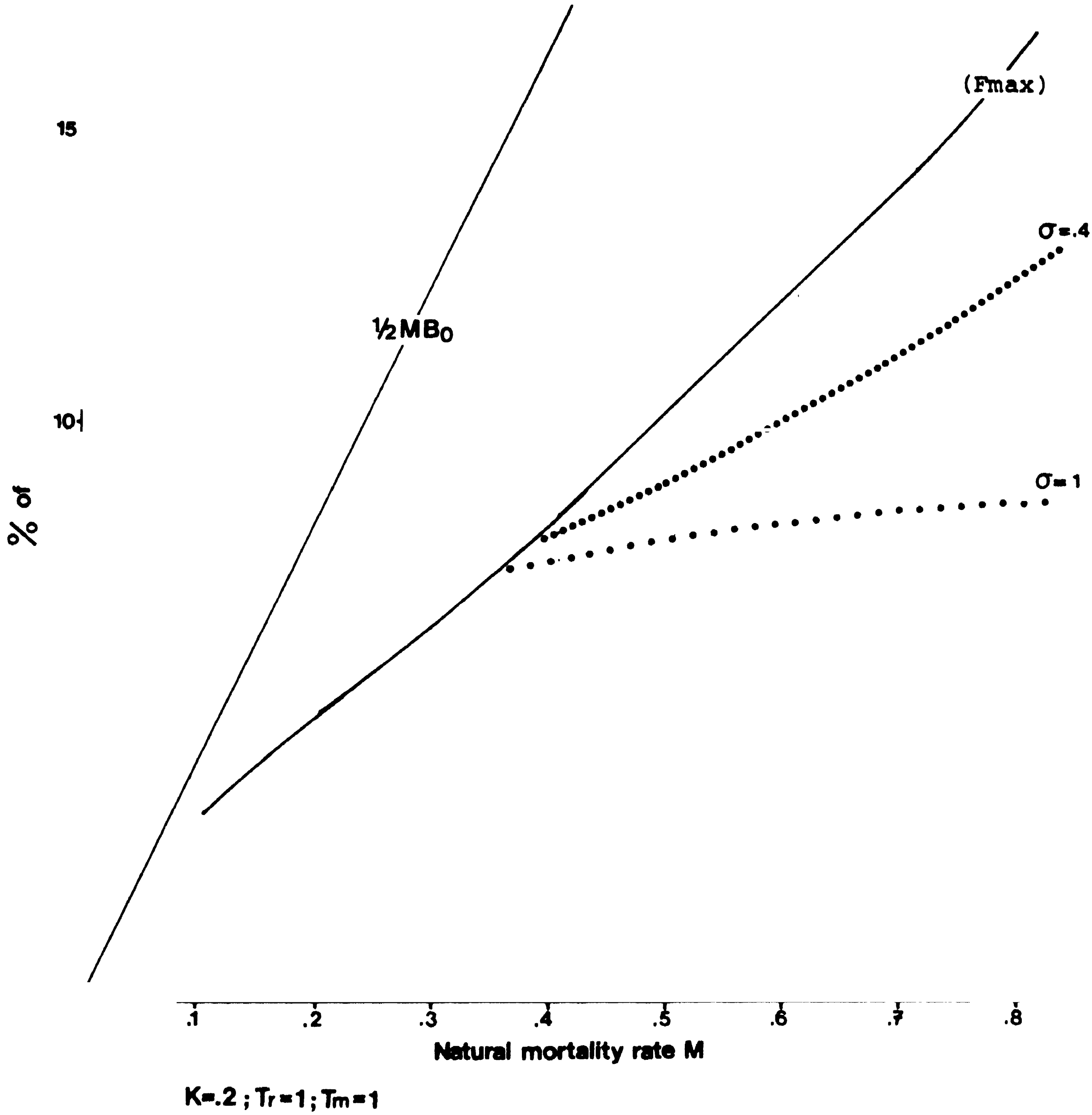


Fig. 12

Potential yield as a percentage of B_0 subject to the constraint that the spawning stock biomass remains above 20% of the unexploited level in a 20 year period with a probability of 90%.

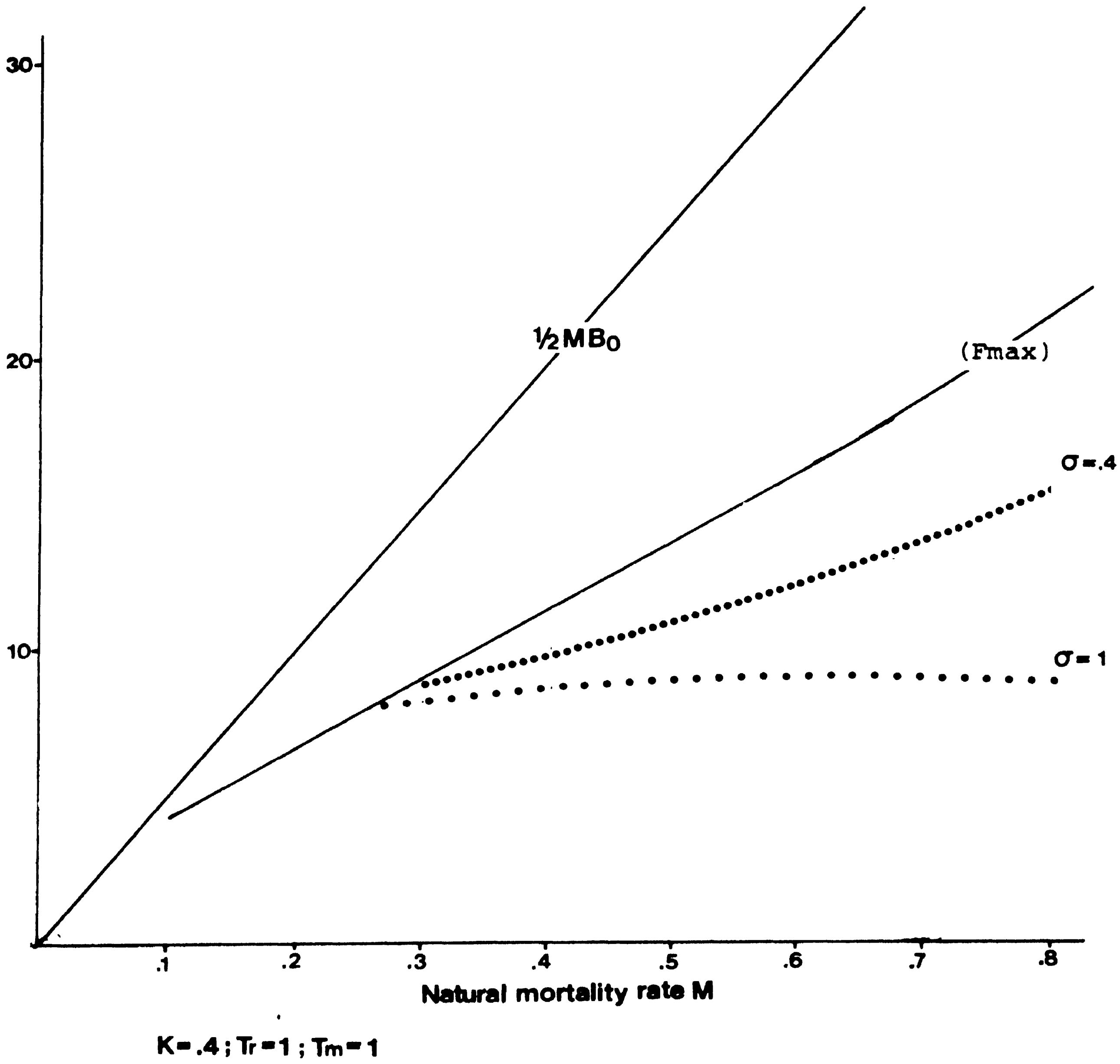


Legend:

(Fmax) = Unconstrained MSY.
.. = Constrained MSY: σ = 0.4
. = Constrained MSY: σ = 1.0

Fig. 13

Potential yield as a percentage of B_o subject to the constraint that the spawning stock biomass remains above 20% of the unexploited level in a 20 year period with a probability of 90%.

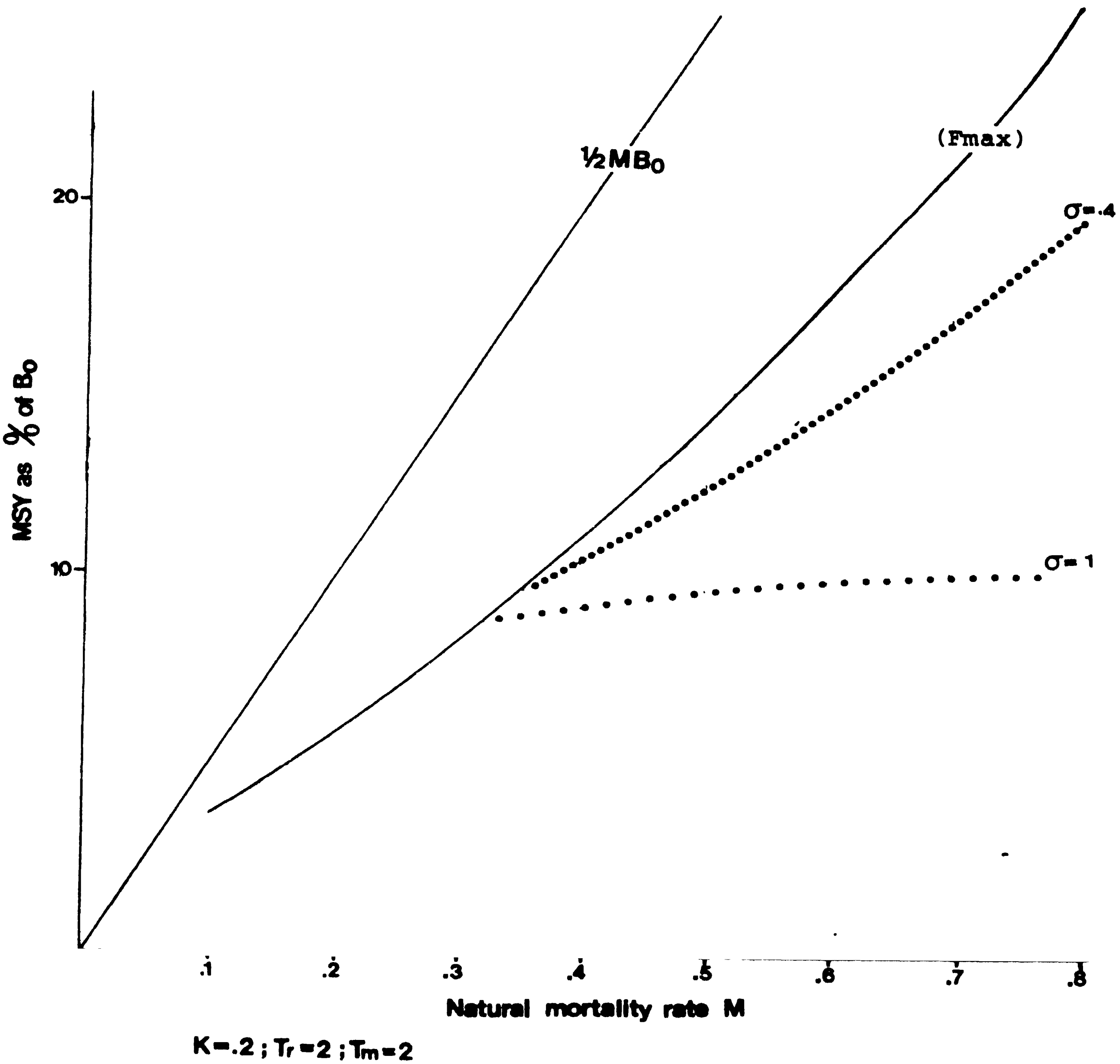


Legend:

(Fmax) = Unconstrained MSY.
.. = Constrained MSY: σ = 0.4
. = Constrained MSY: σ = 1.0

Fig. 14

Potential yield as a percentage of B_0 subject to the constraint that the spawning stock biomass remains above 20% of the unexploited level in a 20 year period with a probability of 90%.

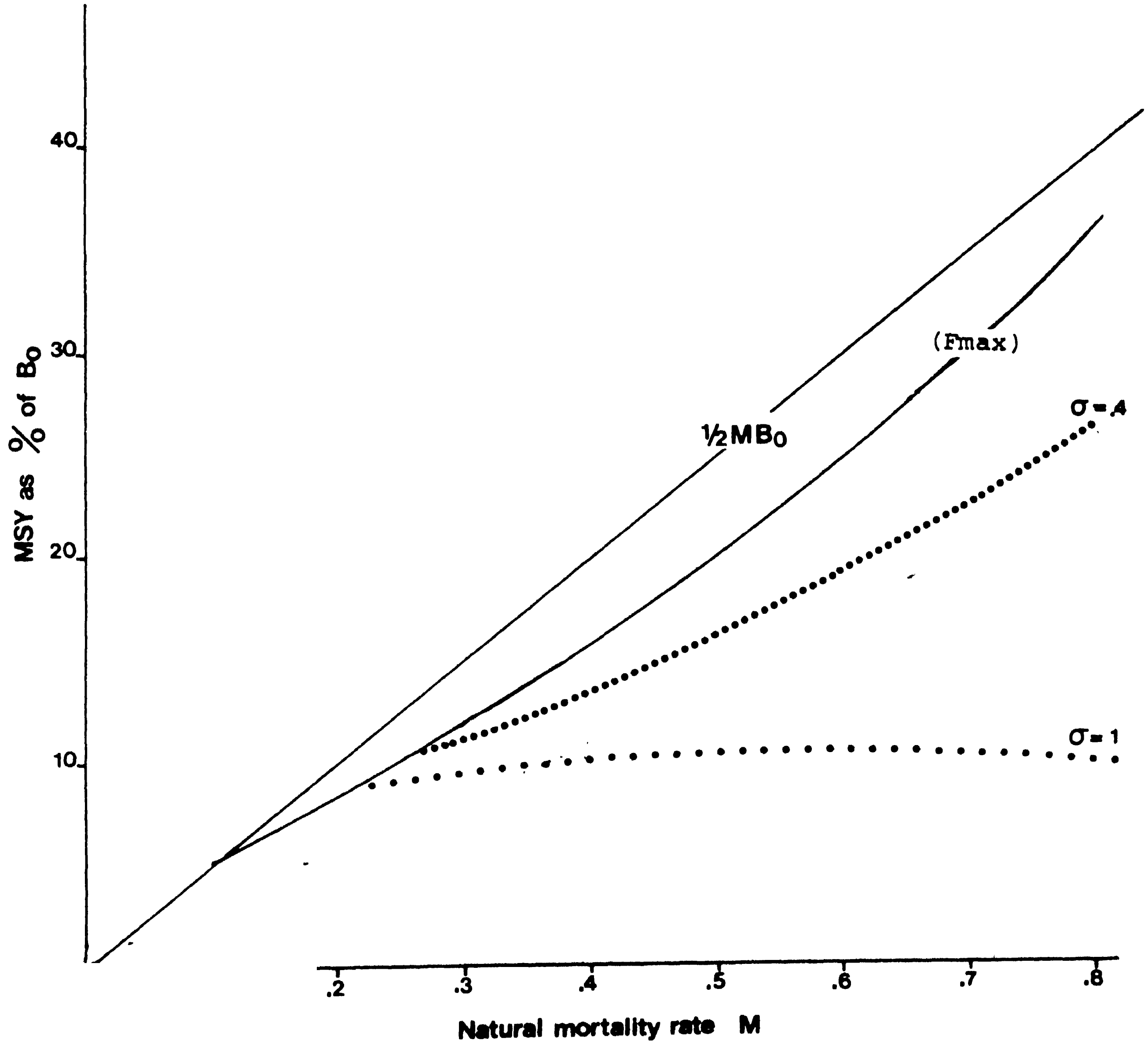


Legend:

(Fmax) = Unconstrained MSY.
.. = Constrained MSY: σ = 0.4
. = Constrained MSY: σ = 1.0

Fig. 15

Potential yield as a percentage of B_0 subject to the constraint that the spawning stock biomass remains above 20% of the unexploited level in a 20 year period with a probability of 90%.



$K=.4;\ T_r=2;\ T_m=2$

Legend:

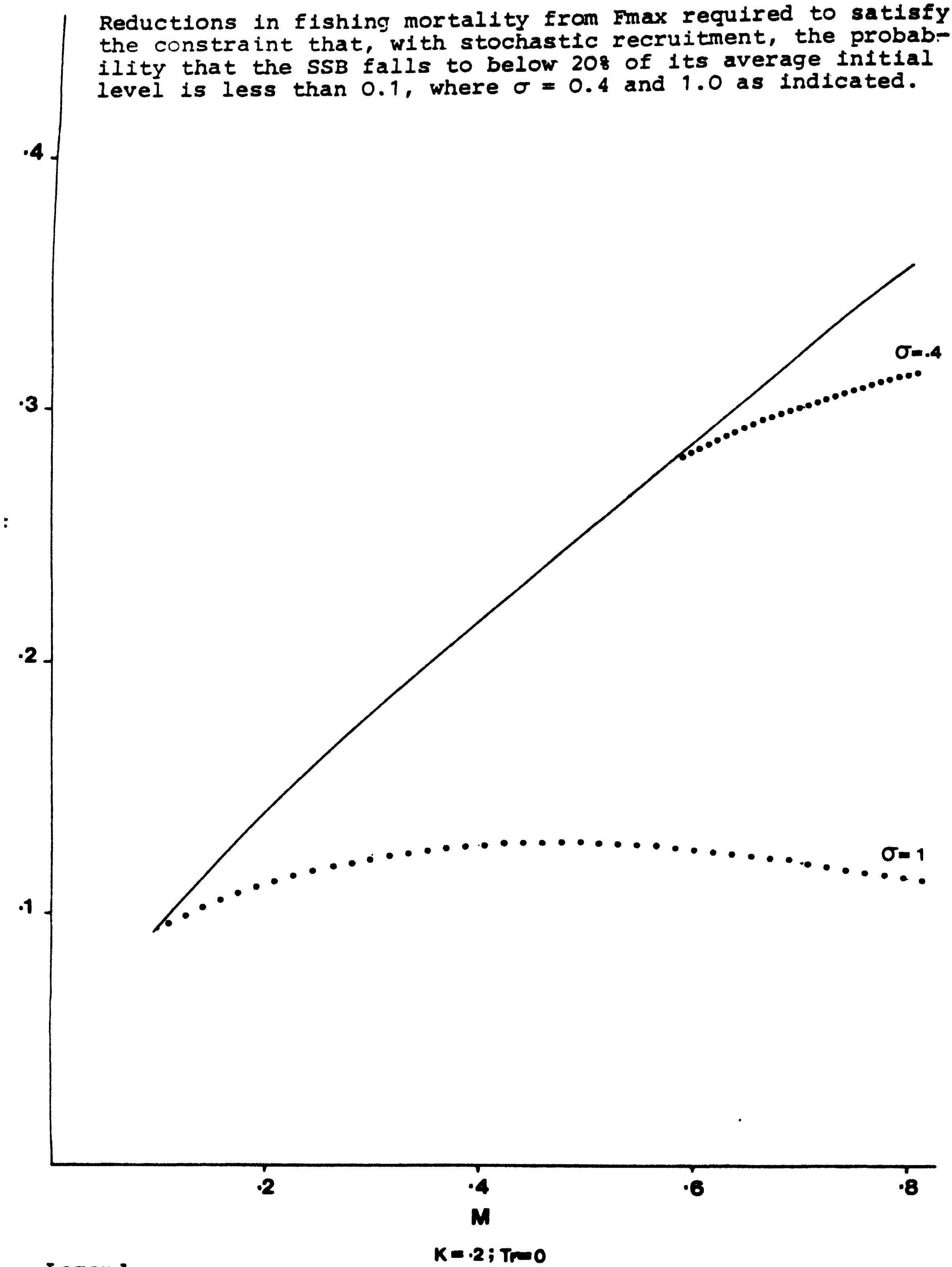
(Fmax) = Unconstrained MSY.

.. = Constrained MSY: σ = 0.4

. = Constrained MSY: σ = 1.0

Fig. 16

Reductions in fishing mortality from Fmax required to satisfy the constraint that, with stochastic recruitment, the probability that the SSB falls to below 20% of its average initial level is less than 0.1, where σ = 0.4 and 1.0 as indicated.



Legend:

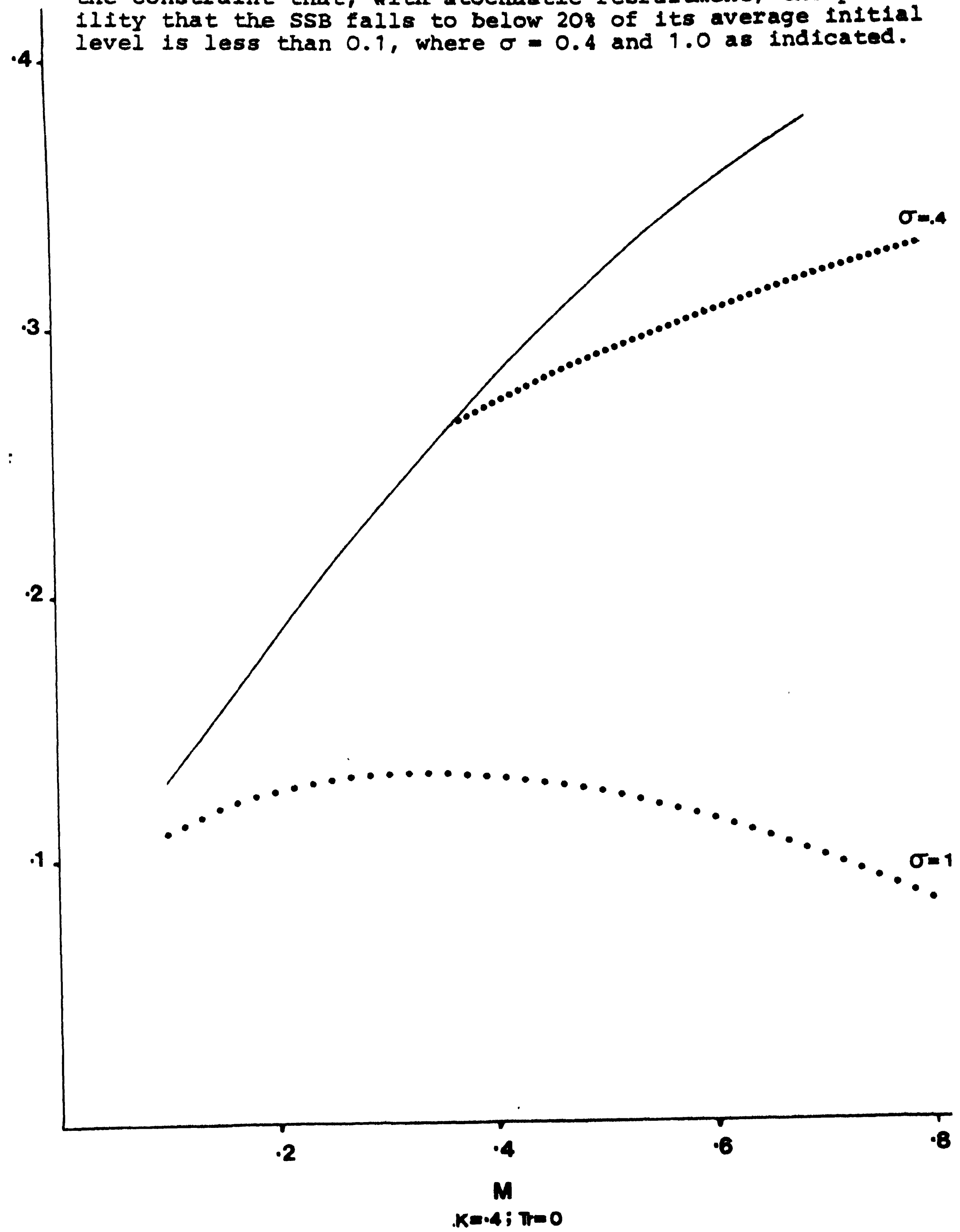
——— = Unconstrained MSY

.... = Constrained MSY: σ = 0.4

. . . .= Constrained MSY: σ = 1.0

Fig. 17

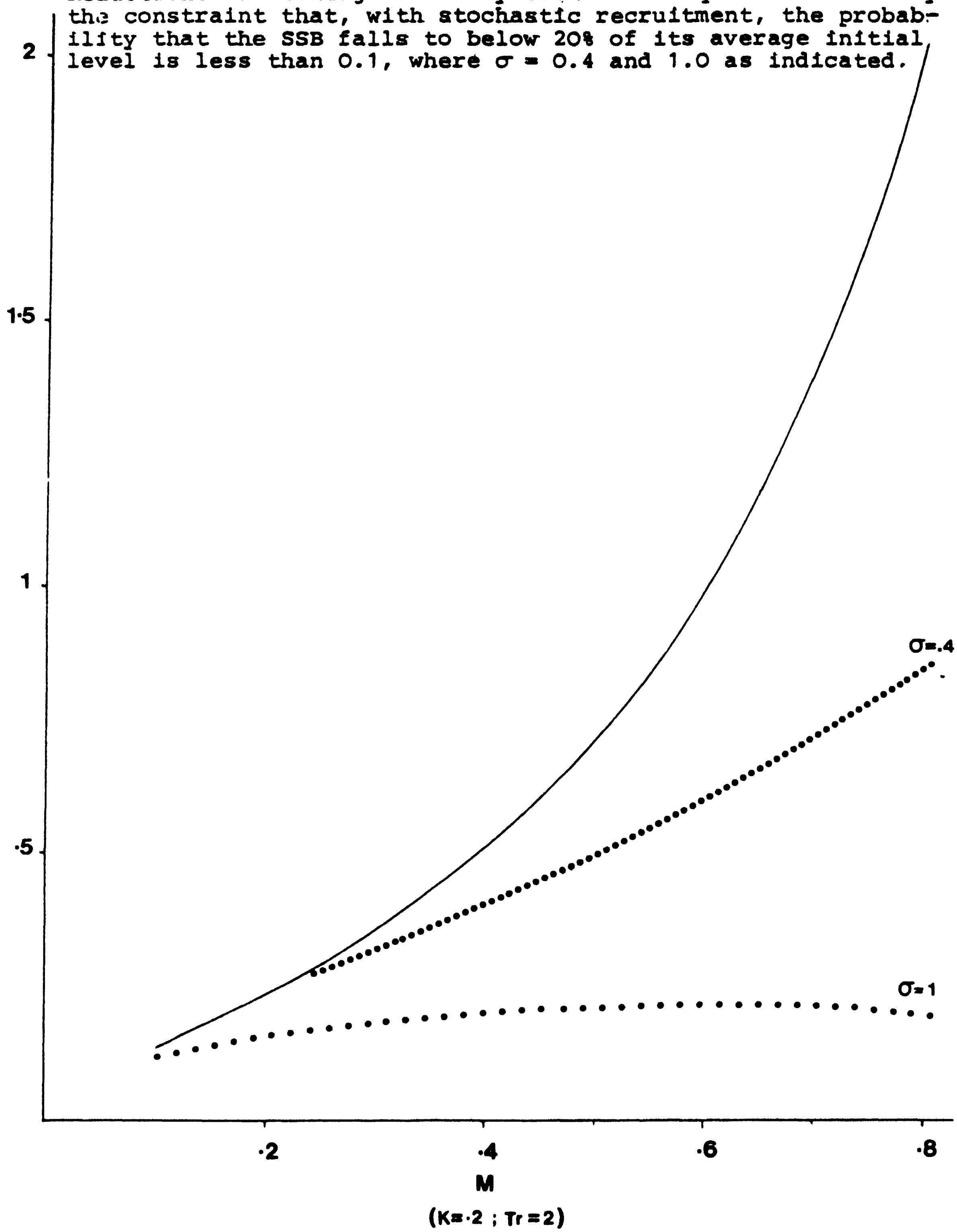
Reductions in fishing mortality from Fmax required to satisfy the constraint that, with stochastic recruitment, the probability that the SSB falls to below 20% of its average initial level is less than 0.1, where σ = 0.4 and 1.0 as indicated.



Legend:
———— = Unconstrained MSY
.... = Constrained MSY: σ = 0.4
. . . . = Constrained MSY: σ = 1.0

Fig. 18

Reductions in fishing mortality from Fmax required to satisfy the constraint that, with stochastic recruitment, the probability that the SSB falls to below 20% of its average initial level is less than 0.1, where σ = 0.4 and 1.0 as indicated.



<u>Legend:</u>

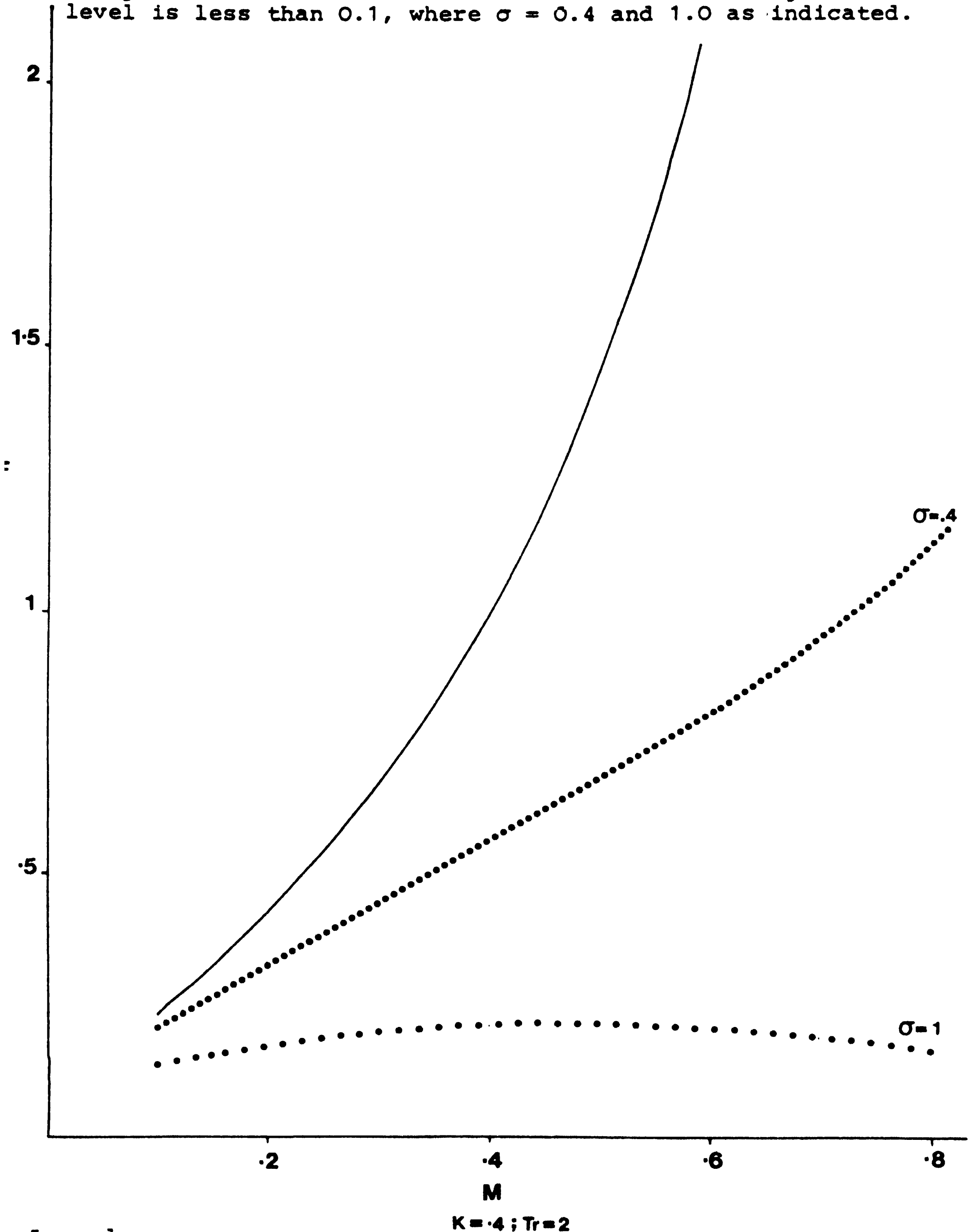
——— = Unconstrained MSY

.... = Constrained MSY: σ = 0.4

. . . .= Constrained MSY: σ = 1.0

Fig. 19

Reductions in fishing mortality from Fmax required to satisfy the constraint that, with stochastic recruitment, the probability that the SSB falls to below 20% of its average initial level is less than 0.1, where σ = 0.4 and 1.0 as indicated.



Legend:

——— = Unconstrained MSY

.... = Constrained MSY: σ = 0.4

. . . .= Constrained MSY: σ = 1.0

Fig. 20 Changes in expected catch levels over time for different levels of fishing mortality. (K=0.4 :M=0.4)

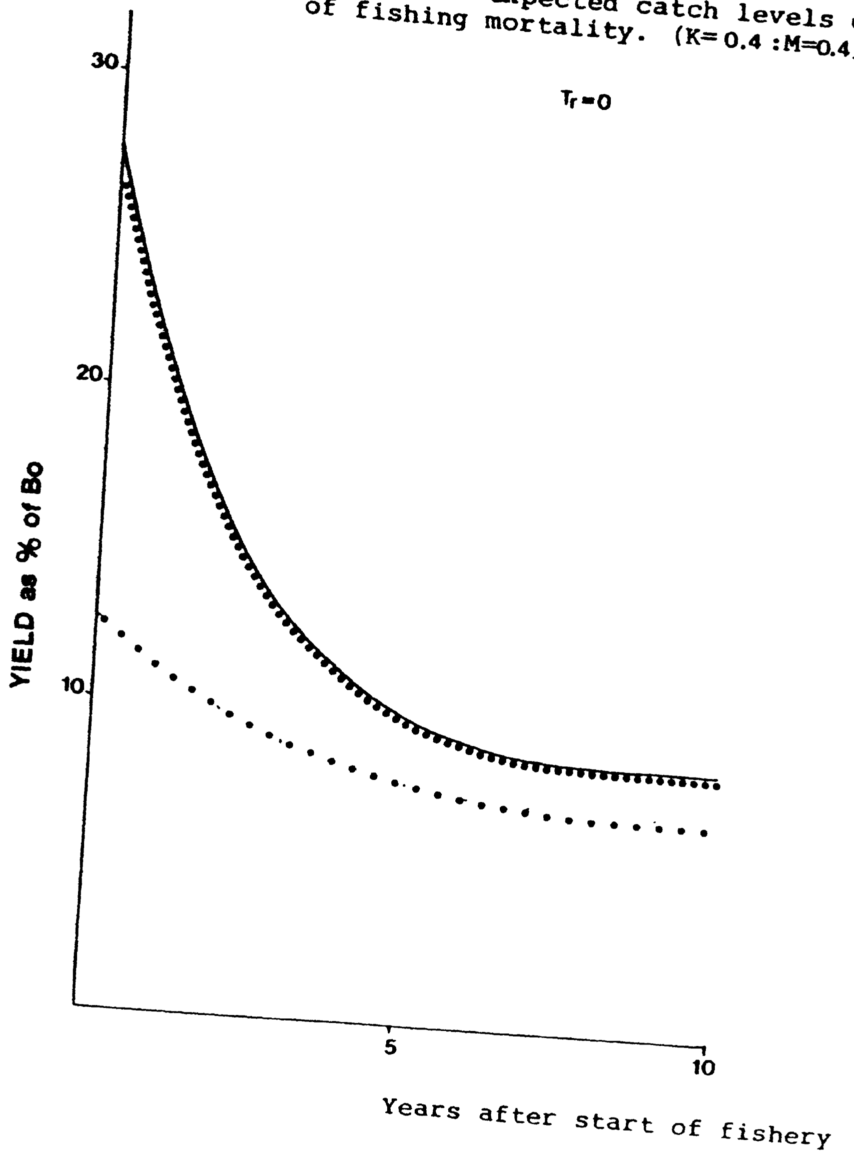


Fig. 21

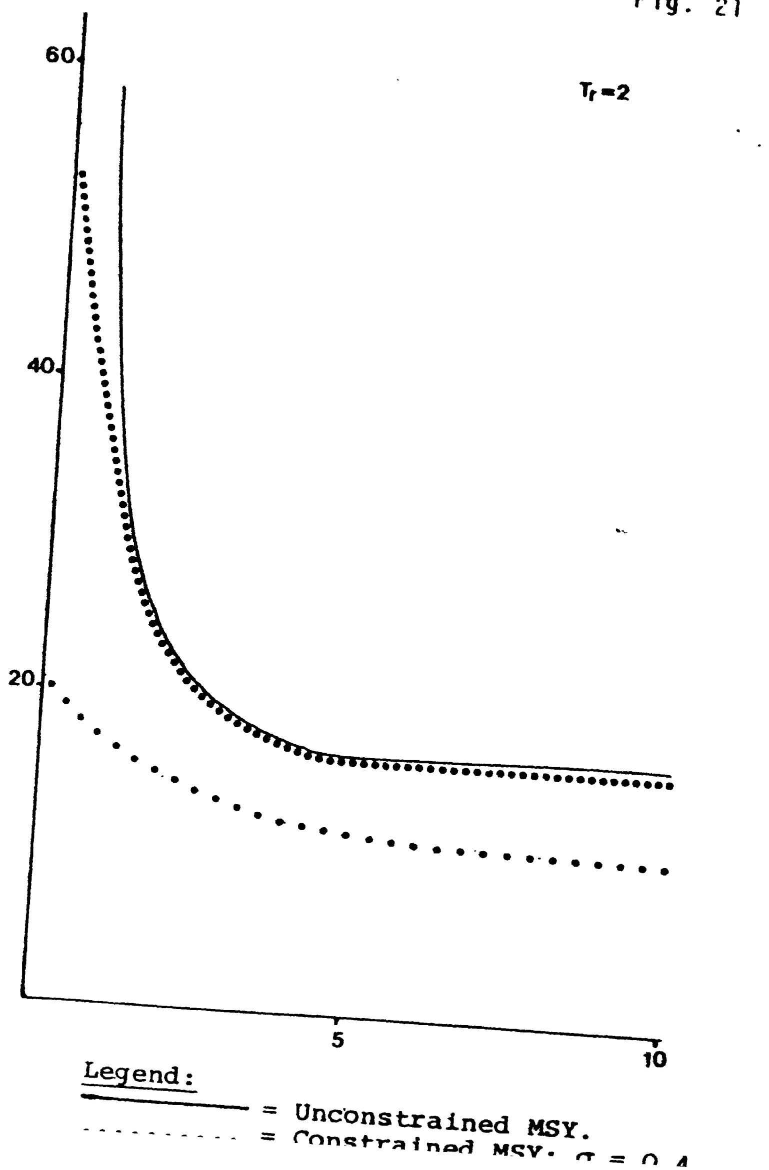
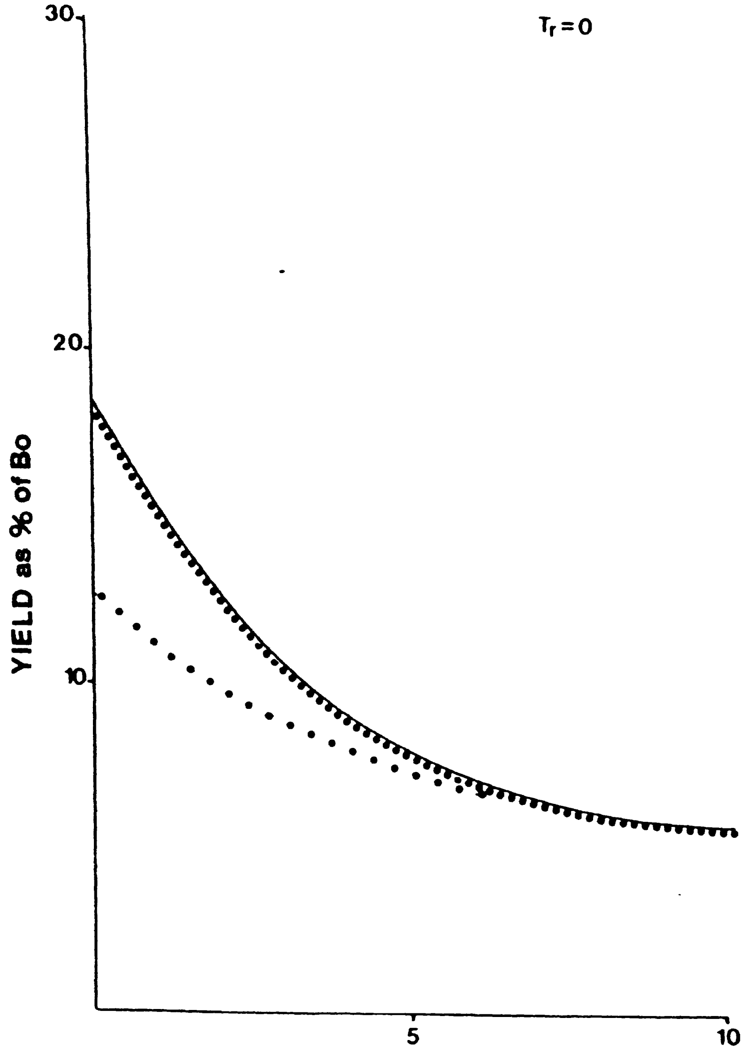
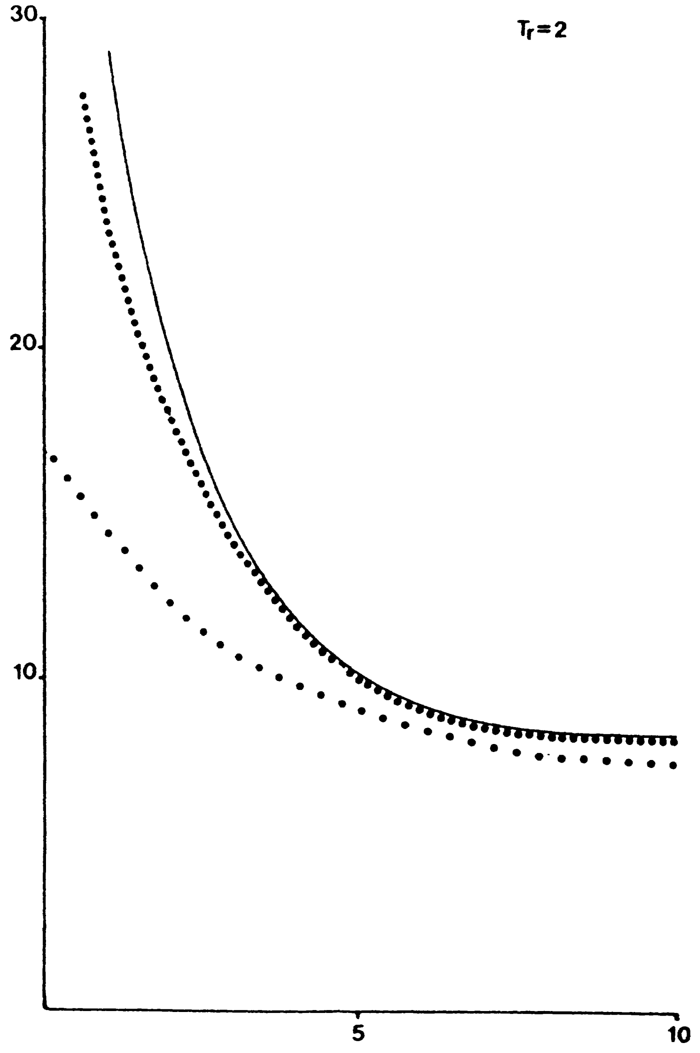


Fig. 22 Changes in expected catch levels over time for different levels of fishing mortality. (K=0.4 :M=0.2) Fig. 23



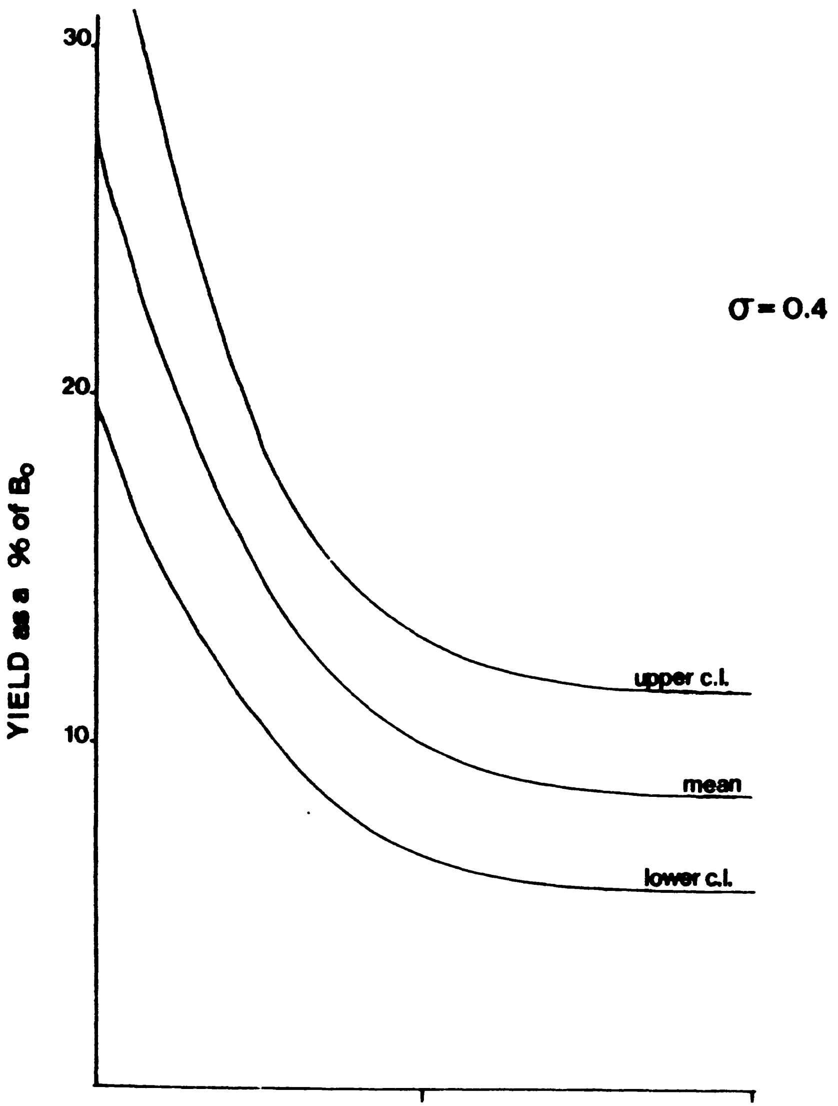


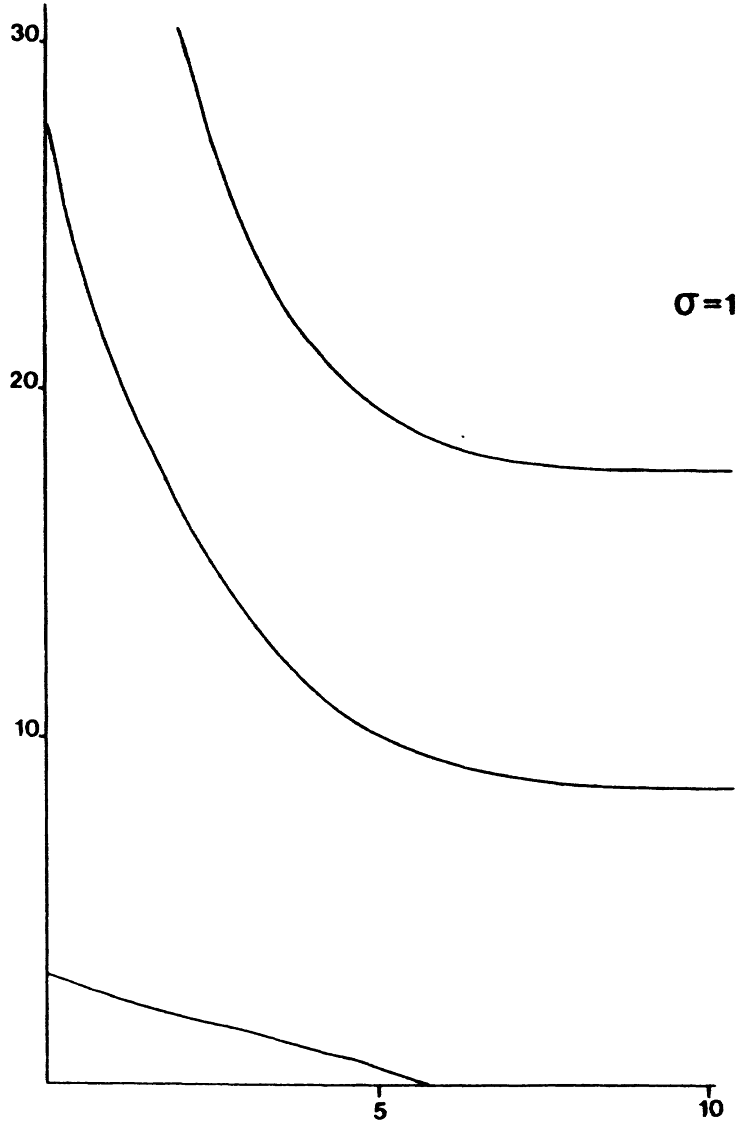
Years after start of fishery

Legend:
———— = Unconstrained MSY.
.... = Constrained MSY: σ = 0.4

Fig. 24 Expected changes in yield with associated approximate 95% confidence regions under constant Fishing Mortality. Fig. 25

($M=0.4$, $K=0.4$, $T_r=0$)





TIME: YEARS AFTER START OF FISHING

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APPENDIX 1

Derivation of maximum yield calculations

The derivation here is essentially the same as that given by Beverton and Holt (1957).

For a recruitment rate, R, at age zero, the number of fish in the unexploited state aged t is Re^{-tM} where M is the natural mortality rate. We assume that the growth follows a von Bertalanffy formula, with a zero weight at age zero, ie:

$$w_t = w_\infty (1 - e^{-kt})^3 \tag{1}$$

where w_t is the weight at age t and w_∞ the asymptotic average weight. This implies that the biomass flux at age t is:

$$Rw_\infty e^{-tM}(1 - e^{-kt})^3 \tag{2}$$

and so the total biomass is:

$$Rw_\infty \int^\infty e^{-tM}(1 - e^{-kt})^3 dt \tag{3}$$

which is equal to:

$$6K^3 Rw_\infty / \{M(M + K)(M + 2K)(M + 3K)\} \tag{4}$$

If we define an age at recruitment, t_r, then the recruited biomass is:

$$Rw_\infty \int_{t_r}^\infty e^{-tM}(1 - e^{-Kt})^3 dt \tag{5}$$

which is equal to:

$$Rw_\infty e^{-t_r M} \left\{ \frac{1}{M} - \frac{3e^{-kt_r}}{M + K} + \frac{3e^{-2kt_r}}{M + 2K} - \frac{e^{-3kt_r}}{M + 3K} \right\} \tag{6}$$

The equlibrium recruited biomass under constant fishing mortality F is thus:

$$Rw_\infty e^{-t_r M} \left\{ \frac{1}{Z} - \frac{3e^{-kt_r}}{Z + K} + \frac{3e^{-2kt_r}}{Z + 2K} - \frac{e^{-3kt_r}}{Z + 3K} \right\} \tag{7}$$

where $Z = M + F$.

The age at recruitment t_r that should be used in this formula is that referred to the theoretical age at zero weight extrapolated from the von Bertalanffy growth curve. If this is non-zero, then the value for t_r to be put in this formula will not be the actual age at recruitment.

If the fishing mortality rate is constant, then the catch rate will be:

$$FRw_\infty e^{-t_r M} \left\{ \frac{1}{Z} - \frac{3e^{-kt_r}}{Z + K} + \frac{3e^{-2kt_r}}{Z + 2K} - \frac{e^{-3kt_r}}{Z + 3K} \right\} \qquad (8)$$

If the catches occur discretely, that is, are confined into short annual seasons, during which the growth and natural mortality rates can be assumed to be negligible in comparison, then the annual catch is:

$$(1 - e^{-F}) Rw_\infty e^{-t_r M} \left\{ \frac{1}{1 - e^{-z}} - \frac{3e^{-kt_r}}{1 - e^{-(z+k)}} + \frac{3e^{-2kt_r}}{1 - e^{-(z+2k)}} - \frac{e^{-3kt_r}}{1 - e^{-(z+3k)}} \right\} \qquad (9)$$

In compiling figures 1-9 and the tables in Appendix 2, formula (8) rather than (9) has been used.

Equation (8) can also be expressed in terms of the length at recruitment. If c is the length at recruitment as a proportion of the average maximum length, then the yield is:

$$FRw_\infty (1 - c)^{M/K} \left\{ \frac{1}{Z} - \frac{3(1 - c)}{Z + K} + \frac{3(1 - c)^2}{Z + 2K} - \frac{(1 - c)^3}{Z + 3K} \right\} \qquad (10)$$

To find the maximum yield for a given length or age at recruitment, we simply maximise (8) or (10) over F. If c is less than the eumetric length c' (the length at which growth and natural mortality exactly balance) given by:

$$c' = \frac{3}{3 + M/K} \qquad (11)$$

then the yield is obtained for a finite value of F. There is no simple formula for F_{max}, but it can easily be evaluated numerically or graphically by plotting a yield versus F curve, such as the one in Figure 10a. Such curves are often rather flat-topped, with a whole range of F values either side of F_{max} all giving much the same yield.

If c is greater than c', then the yield increases asymptotically to a maximum value as F increases.

The theoretical maximum yield obtainable in terms of the recruited unexploited biomass, B_o, from these formulae is MB_o, but this will only be achieved at very high ages or lengths at recruitment and in practice the yields will be much less. Figures 1-5 show the maximum yields as a proportion of B_o for various parameter values.

The maximum yield as a proportion of total initial biomass is given in figures 6-9, for various parameter values. The maximum possible value is achieved by eumetric fishing, ie. where c = c' and F is very large. The yield is then $\alpha_{max}MB_o$, where:

$$\alpha_{max} = \frac{9}{2}(1 - c')^{\mu}(1 - c' + \tfrac{2}{9}c'^2) \qquad (12)$$

where $\mu = M/K$.

If $c > c'$, the yield is αMB_o, where:

$$\alpha = \frac{c^3}{6}(1 - c)^{\mu}(1 + \mu)(2 + \mu)(3 + \mu) \qquad (13)$$

If $c < c'$, there is no simple exact formula for α, but it can be approximated to within +/- 10% by the formula:

$$\alpha \simeq \frac{\alpha_{max}}{2}(1 + c/c') \qquad (14)$$

In most cases c will be less than c', often much less.

The spawning stock biomass corresponding to a given level of fishing mortality is:

$$Rw_\infty\int_{t_m}^{\infty} e^{-(t-t_r)F}\, e^{-tM}\,(1 - e^{-kt})^3 dt \qquad (15)$$

where t_m is the age at sexual maturity. If $t_m > t_r$, which will nearly always be the case in practice, then the spawning stock biomass is equal to:

$$Rw\, e^{-t_rM}\, e^{-(t_m-t_r)F}\left\{ \frac{1}{Z} - \frac{3e^{-kt_m}}{Z + K} + \frac{3e^{-2kt_m}}{Z + 2K} - \frac{e^{-3kt_m}}{Z + 3K} \right\} \qquad (16)$$

<u>Variable recruitment</u>

If we suppose that the recruitment rate is a random variable, with successive annual recruitments independently and identically distributed about a mean R with a coefficient of variation s (ie a variance of R^2s^2) then from equation (5) the variance of the recruited biomass is:

$$R^2 s^2 w_\infty^2 \int_{t_r}^{\infty} e^{-2tM}(1 - e^{-Kt})^6 dt \qquad (17)$$

The integral can be expanded in an analogous form to (6). Likewise analogous formulae to (6) - (10) can be obtained for the variances of the different quantities.

A statistic of interest is the coefficient of variation of the catch and biomass under fishing at constant F, which can easily be calculated from these formulae. In practice, the parameter s will not be known with any precision, and an approximate version of the formula for the co-efficient of variation will suffice. The approximation:

$$\text{c.o.v.} = \frac{2}{3} s \sqrt{Z} \qquad (18)$$

holds quite well for all parameter values and can be applied to the catch, the recruited biomass, or the spawning stock biomass.

The variation in recruitment is expressed in Table 2 in terms of a slightly different statistic, the standard deviation of the log-recruitment, σ. If the log-recruitment is normally distributed then s is related to σ through the formula:

$$s^2 = e^{\sigma^2} - 1 \qquad (19)$$

Equation (18) should be used cautiously for three reasons. Firstly, recruitment in fish stocks tends to have a very skewed distribution and so the confidence limits on the catch and biomass will be asymmetrical. Secondly, in most fish stocks, successive annual recruitments are not mutually independent, but show a strong serial correlation. Even relatively weak serial correlation will invalidate (18). Thirdly, the sample sizes will generally be too small to estimate s or σ to any degree of precision, and this will be exacerbated by any serial correlation that may be present.

APPENDIX 2

Table 1: Maximum sustainable yields expressed as a proportion of the unexploited recruited biomass, for different ages of recruitment, natural mortality rates, and values of the von Bertalanffy growth parameter, K.

AGE AT RECRUITMENT: 0

K \ M	.1	.2	.3	.4	.5	.6	.7	.8
.1	.021	.033	.045	.056	.067	.078	.088	.099
.2	.027	.042	.055	.067	.078	.090	.101	.112
.3	.032	.049	.063	.076	.088	.100	.112	.123
.4	.036	.055	.070	.084	.097	.110	.122	.134
.5	.039	.060	.077	.091	.105	.118	.131	.143

AGE AT RECRUITMENT: 1

K \ M	.1	.2	.3	.4	.5	.6	.7	.8
.1	.023	.037	.052	.068	.085	.103	.122	.143
.2	.030	.049	.067	.085	.105	.125	.147	.171
.3	.036	.059	.080	.101	.123	.146	.171	.197
.4	.041	.068	.092	.116	.141	.167	.195	.224
.5	.046	.076	.103	.130	.158	.187	.218	.250

AGE AT RECRUITMENT: 2

K \ M	.1	.2	.3	.4	.5	.6	.7	.8
.1	.024	.043	.063	.085	.111	.141	.175	.213
.2	.034	.058	.084	.112	.144	.180	.220	.265
.3	.042	.072	.104	.138	.176	.218	.265	.316
.4	.048	.085	.123	.163	.207	.256	.309	.368
.5	.054	.097	.141	.187	.238	.293	.353	.418

AGE AT RECRUITMENT: 3

K \ M	.1	.2	.3	.4	.5	.6	.7	.8
.1	.027	.049	.075	.107	.145	.190	.243	.304
.2	.038	.069	.104	.145	.193	.249	.313	.385
.3	.048	.088	.132	.183	.241	.307	.381	.458
.4	.056	.105	.159	.219	.287	.362	.441	.522
.5	.064	.121	.183	.253	.329	.409	.492	.577

AGE AT RECRUITMENT: 4

K \ M	.1	.2	.3	.4	.5	.6	.7	.8
.1	.029	.056	.090	.132	.185	.248	.322	.399
.2	.043	.081	.128	.184	.251	.326	.406	.488
.3	.054	.105	.164	.234	.311	.392	.476	.562
.4	.064	.127	.197	.276	.359	.444	.532	.622
.5	.073	.145	.226	.310	.397	.486	.576	.668

AGE AT RECRUITMENT: 5

K \ M	.1	.2	.3	.4	.5	.6	.7	.8
.1	.032	.064	.106	.161	.230	.306	.387	.472
.2	.048	.095	.154	.226	.305	.388	.474	.562
.3	.061	.123	.197	.278	.363	.451	.541	.632
.4	.072	.148	.231	.317	.407	.498	.590	.684
.5	.081	.166	.254	.345	.438	.531	.626	.722

Table 2: As Table 1, but with yields expressed as a proportion of total unexploited biomass.

AGE AT RECRUITMENT: 0

K \ M	.1	.2	.3	.4	.5	.6	.7	.8
.1	.021	.033	.045	.056	.067	.078	.088	.099
.2	.027	.042	.055	.067	.078	.090	.101	.112
.3	.032	.049	.063	.076	.088	.100	.112	.123
.4	.036	.055	.070	.084	.097	.110	.122	.134
.5	.039	.060	.077	.091	.105	.118	.131	.143

AGE AT RECRUITMENT: 1

K \ M	.1	.2	.3	.4	.5	.6	.7	.8
.1	.023	.037	.052	.068	.085	.102	.121	.141
.2	.030	.049	.067	.085	.104	.124	.145	.167
.3	.036	.059	.080	.100	.122	.144	.167	.191
.4	.041	.067	.091	.115	.139	.163	.188	.214
.5	.045	.075	.102	.128	.155	.181	.208	.236

AGE AT RECRUITMENT: 2

K \ M	.1	.2	.3	.4	.5	.6	.7	.8
.1	.024	.042	.062	.083	.107	.132	.159	.187
.2	.034	.057	.081	.107	.134	.162	.191	.220
.3	.041	.071	.099	.129	.159	.189	.219	.249
.4	.048	.082	.115	.148	.181	.213	.244	.273
.5	.053	.093	.130	.165	.200	.233	.264	.293

AGE AT RECRUITMENT: 3

K \ M	.1	.2	.3	.4	.5	.6	.7	.8
.1	.027	.048	.072	.098	.127	.155	.183	.209
.2	.037	.066	.096	.126	.156	.185	.211	.233
.3	.046	.082	.116	.149	.180	.207	.230	.245
.4	.054	.095	.132	.167	.197	.222	.239	.248
.5	.060	.105	.145	.180	.209	.229	.241	.244

AGE AT RECRUITMENT: 4

K \ M	.1	.2	.3	.4	.5	.6	.7	
.1	.029	.054	.081	.110	.138	.164	.183	.193
.2	.041	.074	.106	.137	.163	.182	.191	.191
.3	.051	.090	.125	.155	.176	.186	.187	.180
.4	.059	.102	.138	.164	.178	.182	.177	.166
.5	.064	.111	.146	.167	.175	.173	.165	.151

AGE AT RECRUITMENT: 5

K \ M	.1	.2	.3	.4	.5	.6	.7	.8
.1	.031	.059	.088	.116	.140	.153	.155	.147
.2	.045	.080	.112	.137	.150	.151	.143	.130
.3	.055	.095	.126	.143	.146	.140	.127	.111
.4	.062	.104	.130	.140	.137	.127	.112	.095
.5	.066	.108	.129	.134	.127	.114	.098	.081

Table 3: Equilibrium spawning stock biomass levels under fishing at MSY level expressed as a proportion of the initial spawning stock biomass, for different values of the ages at recruitment and sexual maturity, natural mortality rate (M), and growth rate (K).

AGE AT SEXUAL MATURITY: 0

AGE AT RECRUITMENT: 0

K \ M	.1	.2	.3	.4	.5	.6	.7	.8
.1	.302	.309	.311	.317	.315	.318	.315	.318
.2	.289	.306	.311	.309	.314	.315	.314	.316
.3	.278	.301	.304	.307	.308	.312	.312	.314
.4	.267	.294	.301	.306	.308	.310	.309	.312
.5	.261	.284	.293	.301	.304	.308	.307	.311

AGE AT SEXUAL MATURITY: 1

AGE AT RECRUITMENT: 0

K \ M	.1	.2	.3	.4	.5	.6	.7	.8
.1	.302	.309	.311	.316	.313	.314	.310	.311
.2	.289	.305	.310	.307	.310	.309	.306	.305
.3	.277	.300	.301	.303	.302	.304	.301	.300
.4	.266	.292	.297	.300	.300	.299	.294	.293
.5	.260	.281	.288	.293	.292	.293	.288	.288

AGE AT RECRUITMENT: 1

K \ M	.1	.2	.3	.4	.5	.6	.7	.8
.1	.295	.293	.292	.288	.283	.277	.270	.261
.2	.275	.281	.282	.277	.269	.263	.255	.246
.3	.257	.266	.268	.263	.257	.250	.242	.233
.4	.240	.253	.254	.250	.244	.237	.228	.219
.5	.222	.240	.241	.237	.231	.223	.214	.205

AGE AT SEXUAL MATURITY: 2

AGE AT RECRUITMENT: 0

K \ M	.1	.2	.3	.4	.5	.6	.7	.8
.1	.302	.307	.305	.306	.297	.293	.281	.274
.2	.287	.300	.300	.290	.287	.278	.267	.258
.3	.273	.290	.285	.279	.271	.264	.253	.243
.4	.259	.278	.275	.269	.260	.251	.238	.229
.5	.250	.262	.259	.255	.245	.237	.224	.216

AGE AT RECRUITMENT: 1

K \ M	.1	.2	.3	.4	.5	.6	.7	.8
.1	.294	.290	.286	.275	.262	.245	.226	.204
.2	.273	.275	.269	.254	.235	.217	.194	.170
.3	.253	.254	.246	.229	.210	.188	.165	.140
.4	.231	.234	.223	.205	.182	.160	.136	.112
.5	.210	.215	.200	.179	.157	.133	.109	.087

AGE AT RECRUITMENT: 2

K \ M	.1	.2	.3	.4	.5	.6	.7	.8
.1	.278	.278	.264	.246	.227	.207	.186	.163
.2	.253	.251	.237	.219	.199	.177	.153	.127
.3	.226	.225	.210	.191	.169	.145	.120	.092
.4	.200	.198	.183	.163	.140	.114	.087	.058
.5	.176	.174	.158	.136	.112	.084	.055	.042

Table 3: (cont.)

AGE AT SEXUAL MATURITY: 3

AGE AT RECRUITMENT: 0

K \ M	.1	.2	.3	.4	.5	.6	.7	.8
.1	.300	.301	.293	.286	.269	.256	.237	.223
.2	.282	.287	.279	.261	.249	.233	.215	.200
.3	.264	.271	.256	.241	.225	.211	.195	.180
.4	.245	.252	.239	.225	.208	.192	.175	.162
.5	.231	.231	.218	.205	.189	.175	.158	.147

AGE AT RECRUITMENT: 1

K \ M	.1	.2	.3	.4	.5	.6	.7	.8
.1	.292	.283	.271	.250	.226	.198	.169	.139
.2	.267	.260	.243	.216	.186	.158	.128	.100
.3	.241	.230	.210	.180	.151	.122	.095	.070
.4	.215	.202	.178	.148	118	092	067	.047
.5	.188	.176	.148	.118	091	066	046	.030

AGE AT RECRUITMENT: 2

K \ M	.1	.2	.3	.4	.5	.6	.7	.8
.1	.276	.270	.244	.211	173	134	095	.058
.2	.246	.231	.201	.163	123	083	048	.021
.3	.212	.193	.157	.117	077	043	017	.004
.4	.179	.154	.115	.076	041	016	003	.000
.5	.148	.118	.079	.043	017	003	000	.000

AGE AT RECRUITMENT: 3

K \ M	.1	.2	.3	.4	.5		.7	.8
.1	.264	.252	.223	.193	157		076	.030
.2	.229	.209	.181	.146	106		031	0.000
.3	.188	.170	.138	.100	056		000	0.000
.4	.154	.133	.097	.056	029		000	0.000
.5	.123	.098	.060	.025	000		000	0.000

AGE AT SEXUAL MATURITY: 4

AGE AT RECRUITMENT: 0

K \ M	.1	.2	.3	.4	.5	.6	.7	.8
.1	.296	.290	.275	.259	.235	.216	.191	.174
.2	.273	.269	.252	.226	.208	.187	.165	.149
.3	.249	.246	.223	.201	.179	.162	.143	.128
.4	.226	.221	.200	.180	.160	.142	.123	.110
.5	.209	.196	.176	.158	.140	.124	.108	.096

AGE AT RECRUITMENT: 1

K \ M	.1	.2	.3	.4	.5	.6	.7	.8
.1	.288	.271	.249	.218	.185	.151	.118	.088
.2	.257	.238	.210	.175	.139	.108	.079	.055
.3	.225	.201	.170	.134	.102	.074	.051	.033
.4	.193	.167	.134	.101	.072	.049	.031	.018
.5	.163	.137	.104	.073	.049	.031	.018	.009

AGE AT RECRUITMENT: 2

K \ M	.1	.2	.3	.4	.5	.6	.7	.8
.1	.271	.256	.217	.171	.122	.079	.043	.018
.2	.235	.205	.161	.112	.069	.035	.013	.003
.3	.193	.157	.108	.065	.031	.011	.002	.000
.4	.153	.111	.067	.032	.011	.002	.000	.000
.5	.118	.075	.036	.012	.002	.000	.000	.000

AGE AT RECRUITMENT: 3

K \ M	.1	.2	.3	.4	.5	.6	.7	.8
.1	.259	.235	.187	.133	.077	.029	.004	.000
.2	.215	.174	.121	.065	.021	.002	.000	0.000
.3	.164	.118	.063	.019	.001	.000	0.000	0.000
.4	.120	.070	.023	.001	.000	0.000	0.000	0.000
.5	.082	.033	.003	.000	0.000	0.000	0.000	0.000

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Note:

The documents marked with an asterisk were translated into Chinese for use at a UNDP/FAO training course in fish stock assessment held in Shanghai in 1980.

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$$\begin{array}{r} 47 + 17 \\ \hline 64 \end{array}$$